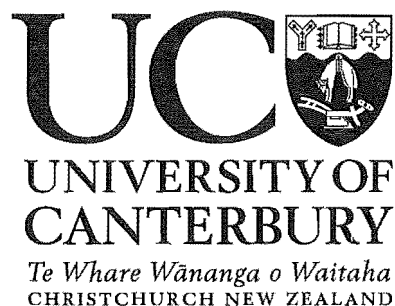


MECHANISMS OF INVASION AND PERSISTENCE OF THE  
INVASIVE KELP *UNDARIA PINNATIFIDA* (HARVEY) SURINGAR  
WITHIN INTERTIDAL AREAS OF SOUTHERN NEW ZEALAND

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Very few studies have examined the mechanisms of local establishment and persistence of invasive marine species, especially invasive seaweeds. *Undaria pinnatifida*, an invasive kelp from Japan, Korea and China was first discovered in New Zealand in 1987. Although *U. pinnatifida*'s spread has been rapid, particularly along the east coast of southern New Zealand very little is known about how this species establishes and persists within invaded areas. This study is unique in that it determines some of the characteristics and mechanisms that enable *Undaria pinnatifida* to invade and persist in intertidal areas of southern New Zealand.

Demographic characteristics of *U. pinnatifida* were examined within the intertidal zone at four sites along the east coast of the South Island, New Zealand. Continual recruitment over this period resulted in the presence of mature plants and recruit plants during most of the year. However, although plants could be found year round at most sites, distinct cohorts were observed between autumn and spring at all sites. Plants were absent during most months of the summer at Rapaki Bay. Maximal growth occurred during the spring but periods of peak growth were variable, both temporally and spatially. Reproducing plants were found from mid winter to mid summer at most sites with peak reproduction occurring between the late spring and mid summer. Potential lifetime reproductive output of individual plants was approximately  $10^8$ - $10^9$  spores and was related to sporophyll size. Plants with the largest sporophylls were found within the low zone at Moeraki Platform. The appearance of spring recruits suggests that autumn recruits may be able to reproduce by winter and provide a second generation during the same year.

Substratum removal experiments examining the ability of *U. pinnatifida* to recruit onto bare space and coralline turfs showed that coralline turfs facilitated recruitment. Large numbers of recruits were found within the coralline turfs regardless of timing of clearance or the size of clearance. Experiments on the survival of early post-settlement stages showed that facilitation may occur by the coralline turfs protecting embryonic sporophytes from harsh physical conditions such as desiccation whereas grazers had no effect on the survival of embryonic sporophytes.

Canopy removal experiments within stands of *Carpophyllum maschalocarpum* revealed that a combination of size and substrata were important in the recruitment

of *U. pinnatifida*. After 12 months, small (5 x 5 cm) clearances had recovered to pre-initiation canopy coverage. In contrast, the medium (25 x 25 cm) and larger (50 x 50 cm) clearances had a mixture of both *C. maschalocarpum* and *U. pinnatifida*. The differences observed between the size treatments were attributed to contrasting life histories and demographic characteristics.

Experimental removal of intra-specific and inter-specific canopies showed that *U. pinnatifida* is capable of recruiting very quickly after a canopy disturbance. This suggests that some form of "seed bank" may be present. Further experiments showed that it was likely the embryonic sporophytes were providing the means for rapid recruitment. Newly-developed embryonic sporophytes placed out in the field were visible after 3 months. This suggests a development period of approximately four months from spore release to visible recruit.

The results from this study suggest that demographic characteristics including rapid growth, high reproductive output and extended recruitment periods are important factors in the establishment and persistence of *U. pinnatifida*. However, life history characteristics including the ability of embryonic sporophytes to delay recruitment and the ability to produce two generations in one year are also considered important. The dominance of *U. pinnatifida* within the intertidal at the study sites is largely due to the ability to coexist with coralline turfs. Coralline turfs appear to facilitate recruitment of *U. pinnatifida* and coupled with its life history and demographic characteristics are probably the reason why *U. pinnatifida* can establish and persist within the intertidal along the east coast of the South Island, New Zealand.

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# **Chapter 1**

## **General Introduction**

## 1.1 Introduction

Coastal marine ecosystems are considered to be among the most invaded ecosystems in the world (Grosholz 2002). In these systems, invasive species, including many seaweeds have been associated with large scale alteration of many communities (Ruiz *et al.* 1997). Consequently, marine invasive species are viewed as an increasingly important component of global change. Yet despite this threat, very little is known about the specific mechanisms involved in the success and failure of species invasions, especially those mechanisms acting at smaller spatial scales. Many studies have focused on the arrival of a new species, the establishment of a population, range expansion and the subsequent ecological impacts of the invasive species, but few studies have examined the mechanisms involved in naturalisation and persistence of invasive populations (Vermeij 1996). This paucity of knowledge is especially evident when dealing with marine ecosystems.

Unfortunately, most studies of marine invasions are inferential and rarely combine extensive descriptive data or experimental results to explain the process of invasion after the initial introduction. As a result, knowledge of the impacts of invasive species in marine ecosystems is relatively poor (Grosholz and Ruiz 1995; Ruiz *et al.* 2000). There are also several inherent difficulties when dealing with invasions in the marine environment. First, the time of invasion may not be known, a problem associated with the lack of historical records (Carlton 1989). Second, the species may be too mobile and therefore difficult to monitor. Finally, dispersal of the species may be difficult to track (as with many small invertebrates). Although these problems make many invasive marine species difficult to study, one group of invasive species which are relatively tractable and are becoming increasingly widespread are invasive macroalgae. Compared to dinoflagellates and most invertebrates, macroalgae tend to be easier to study because of their macroscopic size, the date of invasion is generally known, in most cases their dispersal is limited, and the majority are typically immobile.



## 1.2 Background

Much of the theory on the mechanisms of biological invasions is based on terrestrial and freshwater ecosystems and although some of this may be applied to marine ecosystems there is a shortage of information that confirms this applicability (e.g. Hengeveld 1989; Di Castri *et al.* 1990, Williamson 1996; Perrings *et al.* 2000). Charles Darwin (1859) was possibly the first to put forward an hypothesis on species invasion stating that 'floras gain by naturalisation, proportionally with the number of native genera and species, far more in new genera than in new species' (Origin of species, p114). Since then many explanations and hypotheses have been proposed in an attempt to understand biological invasions. Lonsdale (1999) groups these explanations or hypotheses into three contrasting themes (Table 1.1). The first of these deals with ecosystem properties such as resistance to invasion, the degree of disturbance and fluctuating resource availability (Davis *et al.* 2000). The second theme focuses on the characteristics of the particular species. The third theme places emphasis on dispersal rates and focuses on propagule supply and the rate, quantity and quality of propagules dispersing to a new area (Ruiz *et al.* 2000).

### *Ecosystem properties*

One of the primary hypotheses of invasion biology is based upon the relationship between diversity and invasibility. Elton (1958) is probably the most widely cited author of the diversity-resistance hypothesis which states that communities with high diversity should resist invasion by exotic species more readily than communities with low species diversity. The central idea behind this hypothesis is that when niches are filled and complex trophic interactions are in place (intense competition), there is little ecological space for new colonisers. Although this hypothesis is supported by both theoretical and empirical evidence, there is considerable debate about the relationship between diversity and invasibility (Brown and Peet 2003). Studies conducted at small spatial scales within terrestrial environments suggest that the negative relationship between invader success and diversity is true (Tilman 1997; Tilman *et al.* 1997; Knops *et al.* 1999; Stachowicz *et al.* 1999; Naeem *et al.* 2000; Kennedy *et al.* 2002; Brown and Peet 2003). Other studies, however, have suggested that this relationship is weak and may in fact be positive at larger spatial scales (Levine and D'Antonio 1999; Stohlgren *et al.* 1999; Brown and Peet 2003).

Although there is conflicting evidence for the diversity-resistance hypothesis, the mechanisms driving the relationship are possibly related to competition. Kennedy *et al.* (2002) provided experimental evidence from simplified grassland systems that the mechanism behind highly diverse areas resisting invasion was due to crowding and space limitation. This resulted in intense competitive interactions between resident species. Furthermore, Naeem *et al.* (2000) concluded that inter-specific competition was the cause of the inverse relationship between invader performance and the number of resident species. This conclusion was based on the inability of the invasive grassland weed *Crepis tectorum* to invade diverse assemblages of native grasses in field and laboratory experiments.

Disturbance, as well as being a determinant of community structure in marine systems (Sousa 1980, Dayton 1992), has long been recognised as an important factor in facilitating invasions through the provision of free space (Elton 1958; Crawley 1987a; Hobbs and Mooney 1991). In recent times, the fluctuating resource hypothesis has been put forward, which integrates both disturbance and environmental conditions as a mechanism of invasibility (Davis *et al.* 2000). In plant communities, disturbance usually results in a reduction in the ability of native vegetation to compete and increases the ability of invaders to colonise (Davis *et al.* 1998). The basis of this theory is that a plant community becomes more susceptible to invasion whenever there is an increase in the amount of limiting resources. The assumption is that when resource availability is high, invaders will not encounter such intense competition from native species. Assuming this is true, any factor that increases the availability of a limiting resource will increase the invasibility of a community. Because resource availability fluctuates periodically in any system, the episodic appearance of free space, which is often a limiting resource in marine systems, can result in often dramatic and contrasting patterns of colonisation (Foster 1975; Sousa 1979a; Schiel 1988; Airoldi 2000). Alternatively, variation in disturbance intensity (patch size and shape) may also account for differences in abundance and species composition (Sousa 1979b; Farrell 1989; Benedetti-Cecchi and Cinnelli 1993; Jenkins *et al.* 1999a).

Although hypotheses relating to disturbance and diversity resistance explain some of the habitat features required for successful invasion, they fail to explain why some

species are invasive and others are not. In a recent review, facilitation through positive species interactions was suggested as a possible hypothesis to explain species invasions (Bruno *et al.* 2003). Simberloff and Von Holle (1999) provided numerous examples of exotic plant species that were dependent on indigenous birds and mammals for pollination and dispersal. In the marine environment, many studies have shown that facilitation is an important process in determining community structure (Connell and Slatyer 1977; Camus 1994; Bruno 2000; Bruno and Kennedy 2000; Kennedy and Bruno 2000; Connell 2003). For example, stabilisation of substrata by the intertidal grass *Spartina alterniflora* facilitated the recruitment of a whole suite of indigenous species by buffering seeds and recruits from wave action (Bruno 2000; Bruno and Kennedy 2000; Kennedy and Bruno 2000). However, I am unaware of any species facilitating the establishment of an invasive species within marine ecosystems.

#### *Characteristics of the species*

Many marine studies have examined the importance of life history characteristics and demography on the establishment and persistence of macroalgal populations (Chapman 1984a&b, 1986; Schiel 1985a, 1990; Reed 1990a&b). Ecologists, through manipulation of natural stands or outplanting into natural systems, have found that aspects of their life history and demography such as reproductive output, recruitment, growth, and mortality are important determinants of the ability of a species to establish and persist in often stochastic environments (Black 1974; Schiel and Choat 1980; Schiel 1985a; Schiel and Foster 1986; Reed 1990a; Ang and De Wreede 1992; Reed *et al.* 1996). Studies of life history characteristics have frequently been conducted on invasive species and are thought to provide some predictive power about which species will become invasive (Elton 1958). According to Baker (1974) the ideal weed has the ability to reproduce sexually and asexually, has rapid growth to sexual maturity, phenotypic plasticity, and a broad tolerance of environmental conditions. Over the years this list of characteristics has been added to and modified to include vegetative reproduction, a lack of pre-germination seed treatment (such as stratification or scarification), *r*-selected life history strategies and the ability to switch between *r*- and *k*- life history strategies (Lodge 1993; Daehler and Strong 1996; Kolar and Lodge 2001). These characteristics refer to terrestrial

plants but they can be extended to invasive marine species of most phyla (Crawley 1987a&b).

Although the life history characteristics of a species are deemed important in biological invasions, successful invasion may be due to the absence of natural enemies in exotic environments (referred to as the “enemy release hypothesis”) (Torchin *et al.* 2001; Keane and Crawley 2002). This hypothesis states that any species introduced to an exotic region should experience a release from control by natural enemies such as pathogens, parasites, herbivores or predators (Torchin *et al.* 2001; Keane and Crawley 2002). There are several underlying assumptions to the enemy release hypothesis: natural enemies are important in regulating communities, enemies have a greater impact on indigenous species than exotics, and reduction in enemy regulation allows populations to expand (Keane and Crawley 2002). In marine systems, introduced species may arrive as larvae or propagules and, therefore, are usually free of most adult parasites (Torchin *et al.* 1996). For example, the invasive crab *Carcinus maenas* has invaded substantial areas of the east and west coast of the USA, South Africa, and Tasmania. It was probably introduced as via macroalgal packing that was used to transport oysters. After its establishment, studies showed that parasitic load of *C. maenas* in exotic locations was considerably lower than populations from its native range. Furthermore, in areas where crabs had invaded they grew considerably larger and had a greater biomass (Torchin *et al.* 2001). Although the authors suggested that low parasitic load may have contributed to larger sized crabs other factors such as food quality and environmental conditions may have caused the differences.

### *Propagule pressure*

It is well documented that the dispersal of many invasive species has been aided by humans (Carlton and Geller 1993; Ruiz *et al.* 1997). There is considerable evidence that the transoceanic spread of invasive species has been assisted by ships releasing ballast water, hull fouling and containment within ship's sea cages (Carlton and Geller 1993). However, other vectors such as aquaculture and the aquarium trade have also been implicated in the spread of species (Carlton and Geller 1993). Although many species are transported globally, very few actually succeed in colonising a new area. Of the few species that are able to colonise, only a small

percentage are considered invasive. Part of the reason that many species do not establish is their inability to provide enough propagules to initiate a viable population. Previous studies on birds have shown that continual introduction of individuals by humans (increased propagule pressure) resulted in the successful establishment and persistence of populations (Williamson 1996, Duncan *et al.* 2003). For invasive marine species, the continual reseeding by exchange of ballast water or the high reproductive output of a species increases the propagule pressure on the environment (Carlton 1996). However, not all species that are continually re-introduced to an area will succeed. For example, unsuccessful attempts were made to reseed the heavily fished populations of abalone (*Haliotis rufescens*) in California (Tegner and Butler 1985). Abalone seed 2- 3 cm in size were used but intense predation by octopuses resulted in less than 3% survival of seed over 2 years (Tegner and Butler 1985). This suggests that post-settlement processes may have a significant effect on whether a species will become invasive.

**Table 1.1: Summary table of themes and hypotheses relating to invasion biology with key references.**

Theme	Hypothesis	Key References
<i>Ecosystem properties</i>	Diversity resistance	Elton 1958
		Lodge 1993
		Williamson 1996
		Levine and D'Antonio 1999
	Disturbance	Elton 1958
		Crawley 1987a
	Fluctuating resources	Hobbs and Mooney 1991
		Davis <i>et al.</i> 2000
Facilitation	Simberloff and Von Holle 1999	
	Bruno <i>et al.</i> 2003	
<i>Propagule pressure</i>	Propagule supply, frequency and condition	Carlton 1996
		Williamson 1996
<i>Characteristics of the species</i>	Life history characteristics	Elton 1958
		Baker 1974
		Crawley 1987b
		Lodge 1993
	Enemy release	Torchin <i>et al.</i> 2001
		Keane and Crawley 2002

### 1.3 Invasive species

There are an increasing number of reports of exotic seaweeds being introduced to foreign shores. Some have been introduced intentionally for aquaculture use while others have been accidentally introduced via shipping (Carlton 1989). The list of invasive seaweeds includes species such as *Sargassum muticum*, *Caulerpa taxifolia*, *Caulerpa racemosa*, *Codium fragile tomentosoides*, and *Grateloupia turuturu* (but incorrectly named as *Grateloupia doryphora* in Atlantic areas) (Gavio and Fredericq 2002) (see Table 1.2 for references). However, of all the seaweeds that have extended beyond their natural range none have been studied more than the large fucalean *S. muticum*, the green alga *C. taxifolia* or the laminarian *Undaria pinnatifida*.

*Sargassum muticum* has a long history as an invasive species. It was introduced to the Pacific Coast of North America (*circa* 1940) (Ambrose and Nelson 1982) and Europe (*circa* 1970s) (Farnham *et al.* 1973; Jones and Farnham 1973) via the importation of the Japanese oyster (*Crassostrea gigas*) (Druehl 1973). Since its introduction to these areas much of the literature has focused on its spread (Boalch and Potts 1977; Deysher and Norton 1982; Critchley 1983 a&b; Critchley *et al.* 1983), competition with other species (Fernández *et al.*, 1990) and demography (Norton 1977; Fletcher 1980; Deysher 1984; Hales and Fletcher 1990).

*Sargassum muticum* spreads over large distances by forming large floating rafts (Norton 1976). Adult plants within these rafts release well-developed germlings. These and other characteristics such as rapid growth, monoecious reproduction, a perennial lifecycle, and ability to establish in most areas enable this species to produce large monospecific stands that can inhibit growth and recruitment of indigenous species (Ambrose and Nelson 1982; Critchley 1983a).

**Table 1.2: A list of some of the most notorious invasive marine algae (excluding *U. pinnatifida*) and their origin and distribution. See also Boudouresque and Verlaque (2002) for an inventory of introduced species in European waters.**

Species	Origin	Distribution	Key references
<i>Caulerpa taxifolia</i>	Aquarium trade	Mediterranean California	Boudouresque 1995 Ceccherelli and Cinelli 1998,1999, 2002 de Villèle and Verlaque 1995 Dumay <i>et al.</i> 2002 Jousson <i>et al.</i> 2000 Meinesz and Hesse 1991
<i>Caulerpa racemosa</i>	Red Sea?	Mediterranean	Ceccherelli and Piazzzi 2001 Piazzzi <i>et al.</i> 2001 Verlaque <i>et al.</i> 2000
<i>Sargassum muticum</i>	Asia	North America Europe	Norton 1976,1977 Ambrose and Nelson 1982 Boalch and Potts 1977 Critchley 1983a &b, 1990 Critchley <i>et al.</i> 1983 Deysher 1984 Druehl 1973 Farnham <i>et al.</i> 1973 Fernández <i>et al.</i> 1990 Hales and Fletcher 1990 Jones and Farnham 1973 Knoepffleur-Peguy 1985
<i>Codium fragile tomentosoides</i>	Japan	Atlantic South Pacific	Trowbridge 1995,1996
<i>Grateloupia turuturu</i> (doryphora)	Japan	Atlantic Mediterranean	Harlin and Villalard-Bohnsack 2001 Simon <i>et al.</i> 2001 Villalard-Bohnsack and Harlin 2001

The chlorophyte *Caulerpa taxifolia* is one of the fastest spreading invasive macroalgae. It was accidentally introduced to the French Mediterranean from a public aquarium in 1984 (Meinesz and Hesse 1991). Its ability to grow vegetatively by stoloniferous growth and also from small fragments meant that its advancement across the Mediterranean was rapid. Within ten years *C. taxifolia* had invaded areas up to 600 km away and covered an area of 1300 ha (Meinesz *et al.* 1993). Consequently, the early research on *C. taxifolia* monitored its spread into new areas

(Meinesz and Hesse 1991; Meinesz *et al.* 1993). However, recent studies have focused on the impacts of *C. taxifolia* on indigenous species, particularly the seagrass *Posidonia oceanica* (de Villèle and Verlaque 1995; Bellan-Santini *et al.* 1996). *C. taxifolia* is a successful invader due to its high rate of vegetative reproduction, its ability to persist throughout the year, its broad temperature tolerance and its ability to synthesise bioactive substances that make it unpalatable to grazers.

#### 1.4 Study species

*Undaria pinnatifida* (Harvey) Suringar or “wakame” is a laminarian alga native to coastal areas of Japan, Korea and China. It occurs from the shallow subtidal to depths of 15 m and can grow to 1- 3 m in total length. Mature plants are conspicuous due to the folded sporophyll at the base of the stipe (Fig. 1.1). In its native range wakame is widely cultivated as a food. Although much interest has focused on the commercial aspects of this species, more recently the literature has been concerned with its spread to other areas of the world including the Mediterranean Sea, the Atlantic Coast of France, Venice, southern Italy, England, Argentina, Tasmania, Victoria, and New Zealand (see Table 1.3 for references) and more recently Spain and California (M. Stuart *pers. com.*)

The mode of transoceanic spread of *U. pinnatifida* has varied. The accidental introduction of *U. pinnatifida* with the Japanese oyster (*Crassostrea gigas*) resulted in established populations in the French Mediterranean (Floc’h *et al.* 1991). *U. pinnatifida* was introduced from the French Mediterranean to the French Atlantic Ocean near Brittany for commercial purposes. It was originally thought that *U. pinnatifida* would not be able to reproduce *in situ* due to the cooler water temperatures of Brittany. Contrary to this belief, self sustaining wild populations of *U. pinnatifida* have since been found at Quessant in the Bay of Lampul (Floc’h *et al.* 1991). The spread of *U. pinnatifida* in the French Atlantic means it is now considered naturalised within the Atlantic flora. (Floc’h *et al.* 1991). The introduction of *U. pinnatifida* to New Zealand and Tasmania was probably the result of ballast water contaminated with gametophytes or hull fouling (Hay and Luckens 1987; Stapleton



1988; Sanderson 1990). Fouling on the hulls of boats has been suggested as the dispersal mechanism of *U. pinnatifida* to England (Fletcher and Manfredi, 1995).



Figure 1.1: An adult *U. pinnatifida* plant with the distinctive midrib and sporophyll. Illustration reproduced from *Seaweeds of New Zealand: an illustrated guide*, with permission from Canterbury University Press (Adams 1994). (Scale bar = 2 cm).

**Table 1.3: Literature review (English) on the ecology of *U. pinnatifida* within its native range and as an invasive species around the world.**

Distribution	Aspects of study	Key references
Japan	Review of <i>U. pinnatifida</i> in Japan	Saito 1975
	Competition with coralline algae in an iron depleted environment	Suzuki <i>et al.</i> 1995
Korea	Subtidal distribution	Kim and Lee 1995
	Growth	Oh and Koh 1996
	Seasonality and subtidal distribution	Kim <i>et al.</i> 1998
China	Subtidal distribution	Zhang <i>et al.</i> 1984
New Zealand	Discovery in Wellington Harbour	Hay and Luckens 1987
	Occurrence	Stapleton 1988
	Dispersal of sporophytes by shipping	Hay 1990
	Seasonality of sporophytes at multiple sites	Hay and Villouta 1993
	Occurrence within Timaru Harbour	Brown and Lamare 1994
	Growth	Stuart <i>et al.</i> 1999
	Natural dispersal, spore survival	Forrest <i>et al.</i> 2000
Tasmania	First occurrence	Sanderson and Barrett 1989
	Distribution	Sanderson 1990
	Grazing, disturbance and competition	Valentine and Johnson 2003
Victoria	First occurrence in Victoria	Campbell and Burridge 1998
	Growth and photosynthetic performance	Campbell <i>et al.</i> 1999
Argentina	Distribution	Casas and Piriz 1996
Southern Italy	Occurrence	Cecere <i>et al.</i> 2000
Venice	Distribution within the lagoon of Venice	Curiel <i>et al.</i> 1998
	Expansion, eradication, competition	Curiel <i>et al.</i> 2002
France	Distribution	Floc'h <i>et al.</i> 1991
	Distribution on the coast of St. Malo	Castric-Fey <i>et al.</i> 1993
	Naturalisation, colonization, competition	Floch <i>et al.</i> 1996
	Growth rate and longevity	Castric-Fey <i>et al.</i> 1999a
	Morphology and growth	Castric-Fey <i>et al.</i> 1999b
South Coast of England	Distribution	Fletcher and Manfredi 1995
	Distribution within the North Atlantic and establishment within the U.K.	Fletcher and Farrell 1998

In New Zealand *U. pinnatifida* was probably introduced by international shipping from Asia (Hay and Villouta 1993). Hay and Luckens (1987) first discovered *U.*

*pinnatifida* in Wellington Harbour in 1987 and found that it had spread to several points around the harbour. After its initial discovery, eradication was deemed to be impossible (Hay and Luckens 1987). Subsequent surveys around New Zealand found that *U. pinnatifida* had spread to Lyttelton Harbour, Timaru, Porirua, Oamaru, Otago and Port Chalmers by 1992 (Fig. 1.2). Since then *U. pinnatifida* has been found at other sites along the east coast of the South Island, Stewart Island, Marlborough Sounds, and the Nelson area (Fig. 1.2). Originally it was thought that it would not spread north of Wellington due to the warmer temperatures, but it was found in the Firth of Thames during 2001 (Fig. 1.2). There is evidence to suggest that boating activity is the mechanism that has allowed *U. pinnatifida* to spread so quickly around the coastline of New Zealand (Hay 1990; Forrest *et al.* 2000).

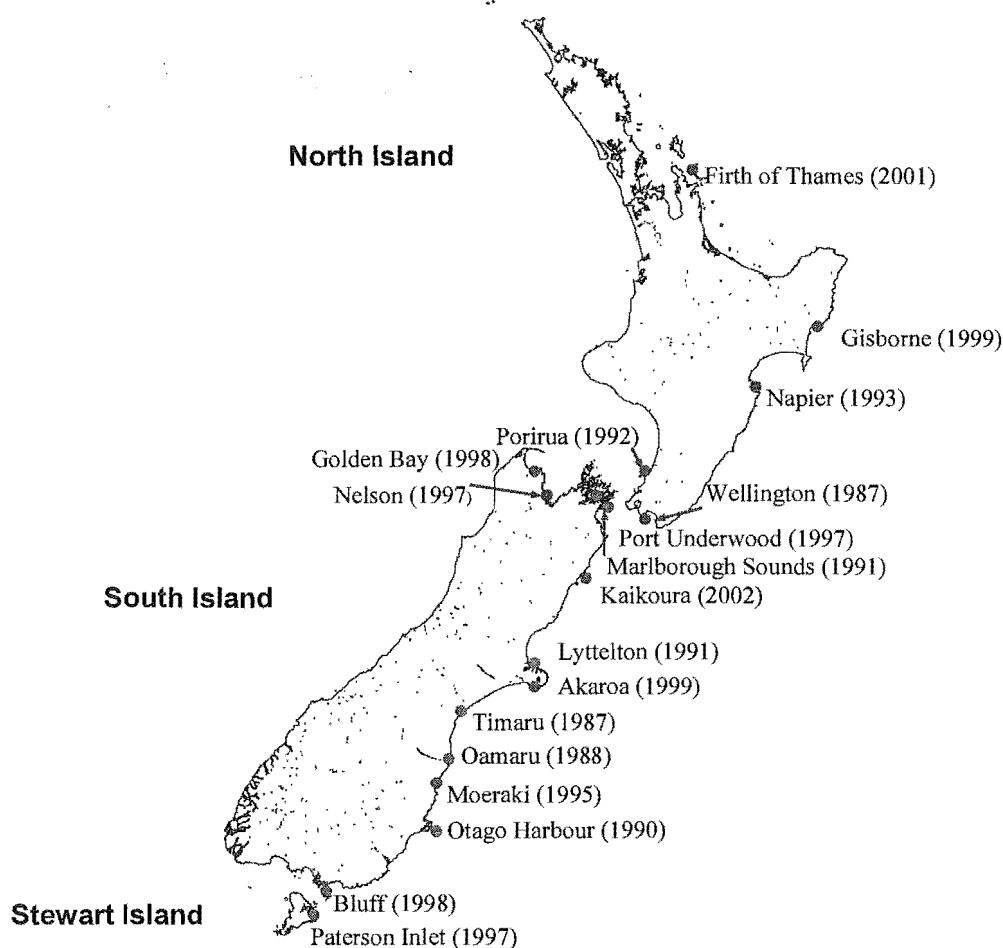


Figure 1.2: Map of New Zealand showing the spread of *Undaria pinnatifida* and the dates it was first discovered (adapted from Forrest *et al.* 2000).

### Life cycle

*U. pinnatifida* is an annual species with a heteromorphic lifecycle, characterised by macroscopic (sporophyte) and microscopic (spore, gametophyte) stages (Fig. 1.3). When zoospores are released they settle onto the substrata within six hours (Saito 1975), but can remain viable for up to 14 days (Forrest *et al.* 2000). Within a day of settling, the zoospores germinate and then develop into haploid male or female gametophytes. The males produce motile sperm that fertilise the non-motile egg within the female gametophyte. The resulting diploid zygote adheres to the substrata either freely or still attached to the female gametophyte. The zygote then develops into the mature sporophyte.

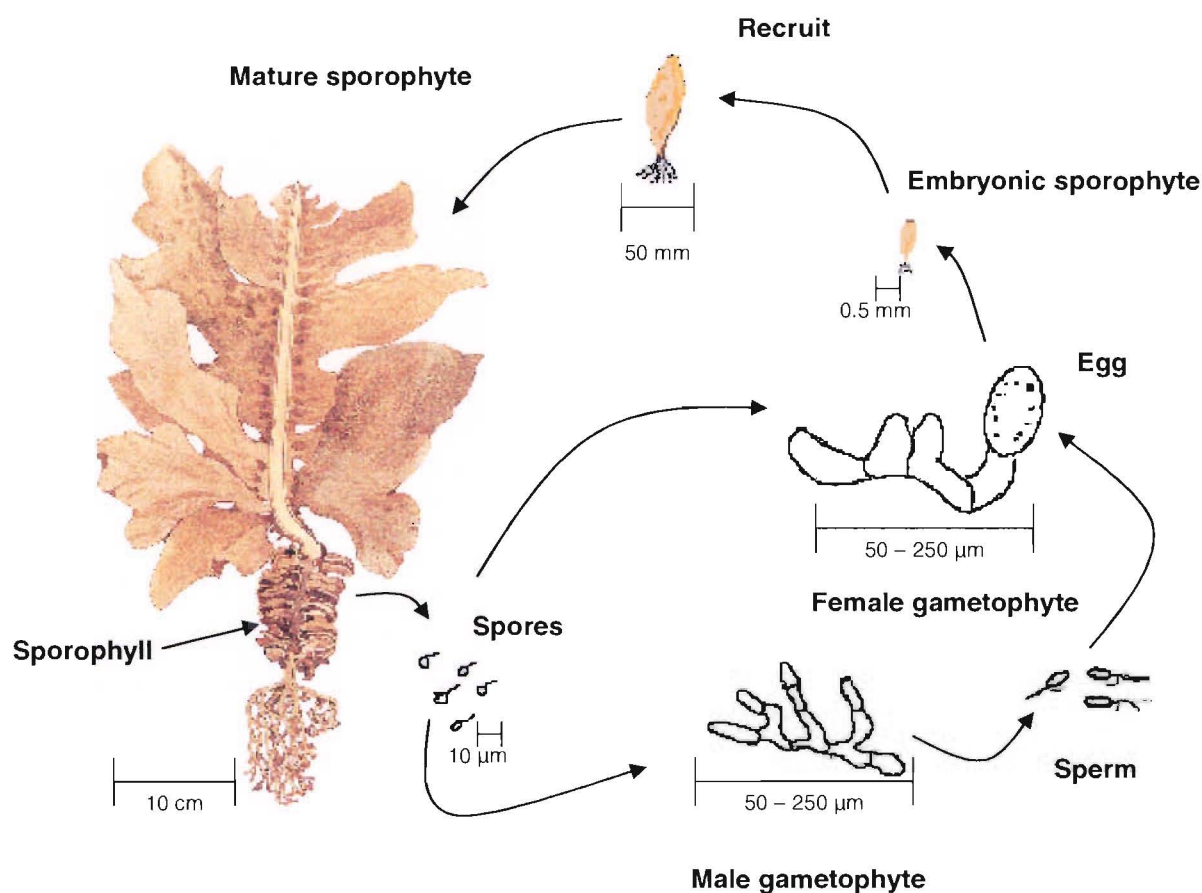


Figure 1.3: Life cycle of the annual laminarian kelp *U. pinnatifida* showing the alternation between the sporophyte and gametophyte stages. Illustration reproduced from *Seaweeds of New Zealand: an illustrated guide*, with permission from Canterbury University Press. (Adams 1994).

In its endemic habitat, and some invaded habitats, sporophytes appear during winter (Saito 1975). Rapid growth occurs from winter to early spring. During spring and early summer, the mature sporophytes release zoospores. At the end of the reproductive phase, adult plants begin to senesce and by late summer macrosporophytes are absent. Recruits begin to appear the following winter. The absence of macrosporophytes during the summer followed by rapid recruitment in the winter is thought to be the result of microscopic stages undergoing vegetative growth or remaining dormant during the summer (Stuart 1997). In some annual laminarian species, the absence of plants between generations has been attributed to a period of vegetative growth of the gametophyte (Clayton 1988; Blanchette 1996). Studies have shown that among laminarian species the gametophyte can undergo vegetative growth during low light conditions (Kain 1964; Kain 1969; Lüning 1980; Novaczek *et al.* 1984a&b). Recent studies, however, have shown that embryonic sporophytes of *Macrocystis pyrifera* can delay development during unfavourable recruitment conditions (Kinlan *et al.* 2003) and this may be the stage that is delayed in *U. pinnatifida*.

Zoospores are formed in the sporophyll that is at the base of the stipe (Figure 1.3). The sporophyll consists of fluted and sinuate thickenings along the edge of the stipe that protrude laterally around the stipe giving it the appearance of a single helix (Hay 1990). Spherical, biflagellate zoospores, 5-6  $\mu\text{m}$  in diameter are produced in small sacs (sporangia) along the margins of the sporophyll. Each sporangium contains 32 zoospores. Zoospore release occurs for several days but only during the daytime. Peaks of 100,000 to 1,000,000 zoospores per 1 g of mature portion of sporophyll can occur each day (Saito 1975).

Previous studies of *U. pinnatifida* outside its endemic range have shown variations in the life cycle from that seen in Asia (Floc'h *et al.* 1991; Hay and Villouta 1993). For example, adult plants and sporelings can be found throughout the year at sites around New Zealand. Hay and Villouta (1993) also noted the presence of overlapping generations with autumn senescent macrosporophytes present with new recruits (Hay and Villouta 1993). It has been suggested that *U. pinnatifida* is not a true annual in New Zealand but rather an aseasonal annual with overlapping generations occurring at the same time (Stuart 1997).

## 1.5 Study sites

My study was done at four sites along the east coast of the South Island, New Zealand (Fig. 1.4). Lyttelton Harbour and Moeraki were chosen as study areas based on the presence of *U. pinnatifida* within the intertidal zone and to give a geographic spread of sites within the South Island. Replicate sites at each area were chosen. Within Lyttelton Harbour, Rapaki Bay and Diamond Harbour were selected. At Moeraki, a north-east facing platform (Moeraki Platform) and rocks next to the beach (Moeraki Beach) were used. Tables 1.4 and 1.5 give a description of the physical attributes and major species present at each site.

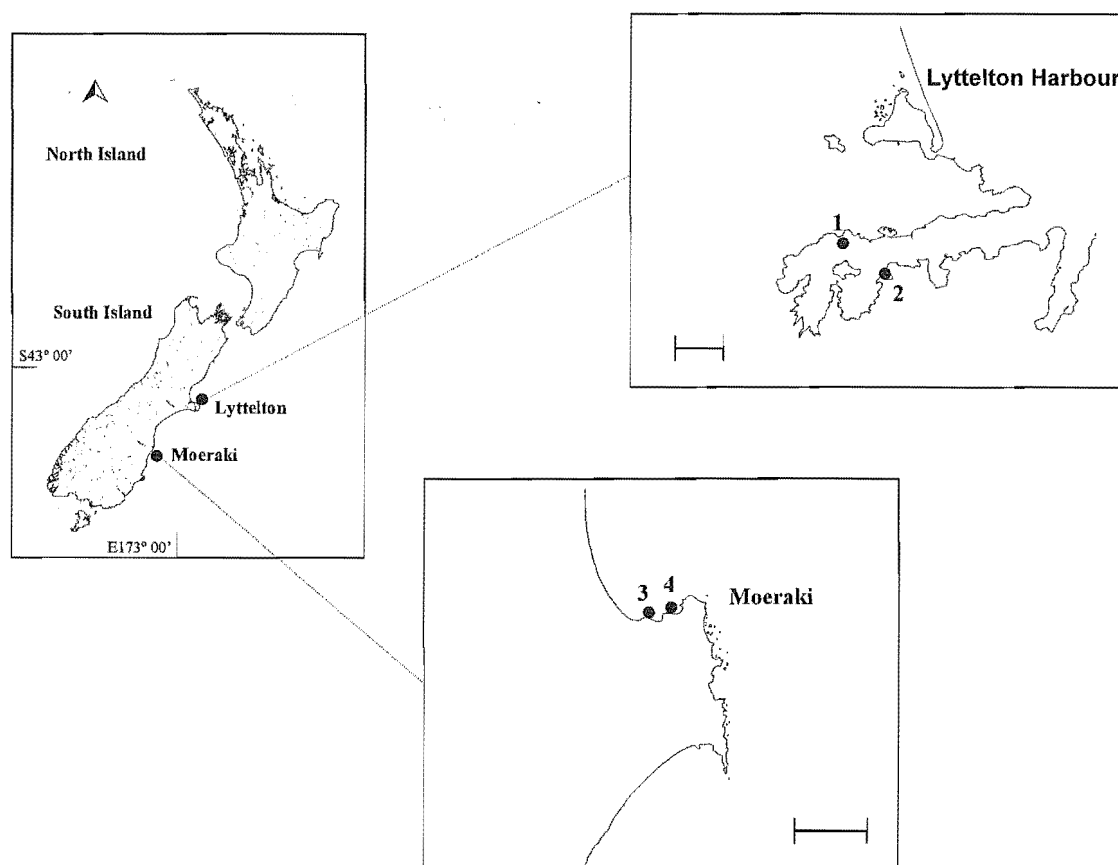


Figure 1.4: Map of New Zealand showing the sites used during the study. The dots represent *U. pinnatifida* populations. 1 = Rapaki Bay; 2 = Diamond Harbour; 3 = Moeraki Platform; 4 = Moeraki Beach. Scale bars  $\approx 5$  km.

Table 1.4 Description of physical attributes of sites used in the study.

Site	Tidal (m)	Range	Rock type	Size (m)	Swell	Slope/Aspect
<b>Diamond Harbour</b> (Low zone)	0 – 2.6		Basalt Boulders	5 x 50	<0.5 m	Gentle South
<b>Rapaki Bay</b> (Low zone)	0 – 2.6		Basalt Platform	5 x 150	<0.5 m	Sharp/Gentle North -east
<b>Moeraki Beach</b> (Low zone)	0 – 2.2		Basalt Boulders	10 x 50	0.5 – 1 m	Sharp/Gentle North
<b>Moeraki Platform</b> (Low zone)	0 – 2.2		Mudstone Platform	5 x 100	0.5 – 1 m	Gentle North-east
<b>Moeraki Platform</b> (Mid zone)	0 – 2.2		Mudstone Platform	8 x 100	0.5 – 1 m	Gentle North -east

Table 1.5 Description of major species found at the study sites.

Site	Dominant algae	Dominant grazers
<b>Diamond Harbour</b> (Low zone)	<i>U. pinnatifida</i> Coralline algae <i>Halopteris congesta</i>	<i>Turbo smaragdus</i> <i>Haliotis iris</i>
<b>Rapaki Bay</b> (Low zone)	<i>U. pinnatifida</i> Coralline algae <i>Carpophyllum maschalocarpum</i>	<i>Turbo smaragdus</i>
<b>Moeraki Beach</b> (Low zone)	<i>U. pinnatifida</i> Coralline algae	<i>Haliotis iris</i>
<b>Moeraki Platform</b> (Low zone)	<i>U. pinnatifida</i> Coralline algae	<i>Turbo smaragdus</i>
<b>Moeraki Platform</b> (Mid zone)	<i>U. pinnatifida</i> Coralline algae	<i>Turbo smaragdus</i>

### 1.5.1 Site Description

#### *Lyttelton Harbour sites*

The Rapaki Bay site consists of a basaltic platform extending around the bay (Table 1.1). Rapaki Bay is on the west side of the harbour and is sheltered from prevailing winds. The bay experiences tidal fluctuations of 2.6 m. The area in which this work was done consisted of a rocky platform approximately 10 m across beyond which the sea bed dropped off into a silty bottom. The low shore is dominated by coralline turfs



and *U. pinnatifida*, although there are small stands of the native fucoid alga *Carpophyllum maschalocarpum* that are present below the coralline turf and *U. pinnatifida* zone. Sedimentation rates are higher at this site compared to the other sites used in this study. Small numbers of *Macrocystis pyrifera* and *Ecklonia radiata* occur subtidally to a depth of approximately 1-2 m.

Diamond Harbour consists of a basaltic platform with medium to large sized boulders interspersed amongst it. Although *U. pinnatifida* normally occupies a narrow tidal range, the uneven topography coupled with the frequent splashing of waves at low tide means that it can occupy areas from 0-0.6 m MLW. The tidal fluctuation at this site is 2.6 m. Moderate swells of 0.5 – 1 m can occur at this site.

#### *Moeraki sites*

Moeraki Platform is an extensive mudstone platform some 200 m wide and 300 m long with a north-east aspect and extends subtidally to a depth of c. 5-6 m. The reef is riddled with small burrowing bivalves (*Pholid* sp.), which make the lower platform very brittle so that sections of rock frequently break off during storms. There are substantial beds of seagrass on the SW edge of the platform. Intermingled within the platform are large tidepools (~ 10 m wide). *U. pinnatifida* occurs subtidally but is most abundant in the intertidal zone from 0 - 0.7 m MLW. The tidal range at this site is 2.2 m. Moderate swells of 0.5 –1 m can occur at this site.

The Moeraki Beach site consists of a rocky outcrop with a northerly aspect. Large boulders and small rocks interspersed amongst a coarse sand beach make up this area. *U. pinnatifida* occupies much of the low zone although other native species such as *Xiphophora gladiata novae-zealandiae* and *Jania novae-zealandiae* are also present. The subtidal area consists of coarse sand. This site is also subjected to moderate swells of up to 1 m.

### 1.6 Study aims

There is extensive literature describing the distribution of invasive algae, but very few studies examine the mechanisms involved in the establishment and persistence of these species once they reach foreign shores. Studying *U. pinnatifida* outside its



native habitat provides an opportunity to test the mechanisms driving successful marine invasions. The sedentary nature of seaweeds allows their distribution and spread to be monitored more easily than mobile species. This thesis examines the small-scale mechanisms of invasion affecting the persistence and spread of the adventive seaweed *U. pinnatifida*. The thesis itself is comprised of a general introduction, four experimental chapters and a general discussion.

Chapter 2: **General demography**, describes and compares the abundance, growth, reproduction, recruitment and survival of *U. pinnatifida* at four sites along the east coast of the South Island, New Zealand. These demographic characteristics are important in understanding the invasion success of *U. pinnatifida* in new habitats. More importantly, by studying the demography of *U. pinnatifida*, predictions can be made about the likely extent of further expansion.

Chapter 3: **Mechanisms of establishment**, examines through field experiments the ability of *U. pinnatifida* to recruit into primary bare space and coralline turf within the intertidal zone. Turfing algae are ubiquitous around the rocky intertidal area of New Zealand and are considered to be major habitat-forming species. Hence, the ability of *U. pinnatifida* to invade these types of habitats after disturbance could have major implications for intertidal ecosystems. Establishment of *U. pinnatifida* in relation to timing and size of disturbance were tested.

Chapter 4: **Canopy disturbance**, experimentally examines the effect of interspecific and intraspecific canopy disturbance on the establishment of *U. pinnatifida*. The ability of *Carpophyllum maschalocarpum* canopy to recover after removal was examined over 1 year. Further experiments were done to examine the interactive effect of *C. maschalocarpum* and coralline turfs on the recruitment of *U. pinnatifida*. Recruit suppression by mature conspecifics was also examined during periods of reproduction and non-reproduction in order to determine whether a 'seed bank' existed.

Chapter 5: **Early post-settlement survival and growth**, investigates post-settlement processes affecting the development and survival of embryonic sporophytes within intertidal habitats. Experiments examined the survival and growth

of embryonic sporophytes under and outside canopies of *C. maschalocarpum* and mature conspecifics. Further experiments were done to examine the effects of macroinvertebrate grazers on survival of embryonic sporophytes. The chapter concludes with experiments examining the growth rates of embryonic sporophytes during winter and summer and the ability of embryonic sporophytes to delay recruitment.

Chapter 6: **General Discussion** synthesises the work from the experimental chapters and discusses the results in relation to the mechanisms involved in the establishment and persistence of *U. pinnatifida* within intertidal areas of New Zealand.

## **Chapter 2**

### **General Demography**

## 2.1 Introduction

Differences in demography and life history strategies are major determinants in controlling the distribution and abundance of seaweeds (Kain 1975; Duggins 1980; Dayton *et al.* 1984; Santelices 1990a&b; Reed 1990a; Reed *et al.* 1997). These differences reflect that marine algae have evolved flexible strategies to cope with variable abiotic and biotic conditions (Reed and Foster 1984; Schiel 1985a; Reed *et al.* 1988; Dayton *et al.* 1992; Reed *et al.* 1997). For some species of marine algae, demographic characteristics and life history features have provided mechanisms for successful invasion of habitats outside their endemic range.

Relatively few invasive macroalgae have been studied but the available information suggests that the success of these species is probably due to a number of demographic processes that include rapid growth, large reproductive output, and high survival of early post-settlement stages (Norton 1976; Fernández *et al.* 1990; Hales and Fletcher 1990; Floc'h *et al.* 1991; Meinesz *et al.* 1993; Ceccherelli and Cinelli 1999). For example, the fucalean *Sargassum muticum* is particularly successful due to its ability to self-fertilise and produce huge numbers of germlings with a broad tolerance to irradiance, temperature and salinity. Under certain conditions, *S. muticum* can shorten its reproductive period and has the ability to retain zygotes on the parent receptacles (Fernández *et al.* 1990). In contrast, the chlorophyte *Caulerpa taxifolia* is thought to be a successful invader due to its ability to survive under a broad range of temperatures, persist throughout the year and to reproduce vegetatively from small fragments (Meinesz and Hesse 1991; Meinesz *et al.* 1993; Ceccherelli and Cinelli 1999).

Laminarian life histories are well known, however, the invasive characteristics of the laminarian kelp *Undaria pinnatifida* are largely unknown. Previous studies have shown that this species has a high reproductive output (Saito 1975), and rapid growth (Floc'h *et al.* 1991). Other studies have suggested that *U. pinnatifida* is successful due to its ability to alter its life history characteristics in new environments (Floc'h *et al.* 1991; Hay and Villouta 1993).

In its native habitats *U. pinnatifida* exhibits a distinct annual cycle with recruits appearing during late autumn (Saito 1975; Koh and Shin 1990). Plants grow rapidly during the late winter and spring, reproduce and then senesce by mid summer. From late summer macroscopic plants are absent until new recruits appear. This can occur for some months until the new recruits appear. In some areas outside its endemic range *U. pinnatifida* is not a strict annual (Floch *et al.* 1991, Hay and Villouta 1993). Hay and Villouta (1993) and Stuart (1997) found mature plants and sporelings throughout the year at many sites around New Zealand. Furthermore, there was an overlapping of generations with senescent sporophytes of one year found with recruits of the next generation. Based on this information, it has been suggested that *U. pinnatifida* is not a true annual in New Zealand but has an aseasonal annual cycle with overlapping generations (Floc'h *et al.* 1991, Hay and Villouta 1993).

In native and invaded areas *U. pinnatifida* is mostly a subtidal species occurring from depths below EMLW-15 m (Sanderson and Barrett 1989). However, in many areas around New Zealand it occurs almost exclusively in the mid to low intertidal zone. The aim of my study was to understand the life history of *U. pinnatifida* within the rocky intertidal zone along the east coast of the South Island, New Zealand. A major portion of this study was an examination of the demographics of the species including growth rates, reproductive periodicity, fecundity, dispersal, recruitment and survival. The data, although largely descriptive, provide insights into how *U. pinnatifida* spreads once it establishes in new areas. Furthermore, results from this work led to several hypotheses that are considered in subsequent chapters.

## 2.2. Methods

Demographic characteristics were sampled at approximately monthly intervals at each of the four sites: Diamond Harbour, Rapaki Bay, Moeraki Beach and Moeraki Platform. Due to the wide distribution of *U. pinnatifida* at the Moeraki Platform the sampling regime was stratified to include the low zone, the mid zone and the upper mid zone. At the other sites *U. pinnatifida* was found predominantly in the low zone.

### 2.2.1. Population structure

To test the hypothesis that population structure of *Undaria pinnatifida* would vary between sites spatial and temporal sampling was done at the four sites. To measure patterns of plant abundance and size structure, ten 0.25 m<sup>2</sup> quadrats were randomly placed each month. Within each quadrat, plants were divided into recruits (plants < 50 mm), immature (plants > 50 mm but with no sporophyll) and mature (plants with a sporophyll) and counted. Recruits, immature and mature plants were summed to provide the total density. All *U. pinnatifida* plants counted were measured *in situ* for total length, stipe width and sporophyll length (if present) (see Fig. 2.1). Total length and sporophyll length were measured to the nearest 5 mm. Stipe width was measured to the nearest 0.05 mm using Vernier calipers. Further quadrats were sampled until 50 plants had been measured. Data were analysed using ANOVA in Statistica 6.0™. Site was used as a fixed factor. Prior to analysis, data were tested for homogeneity of variances using Cochran's test. Appropriate transformations were done as required.

### 2.2.2 Growth

To test the hypothesis that growth rates of *Undaria pinnatifida* would vary between sites plants were randomly chosen and tagged each month between June 2000 and May 2002 within each zone at the four sites. Tags were made using individually embossed 9 mm Dymo tape® and 1 mm diameter plastic-coated copper wire. The wire was threaded through the holdfast of the plant. Plants had to be sufficiently large enough (typically >200 mm) to be tagged correctly. A preliminary trial was undertaken in March 2000 and August 2000 at Diamond Harbour to determine if there would be any significant tag loss. Fifty plants were double tagged and monitored sporadically for 7 weeks. Although there was some tag damage (usually the edges had delaminated) no tags were lost.

Thirty randomly chosen plants were tagged and measured for total length, stipe length, stipe width and sporophyll length if present (Fig. 2.1). The position of plants were mapped. Holes were punched 50 mm above the stipe blade margin on each

side of the blade to measure incremental growth. This method is commonly used when estimating growth of laminarian algae (Mann and Kirkman, 1981). Although it damages plants, it gives a good estimate of blade elongation and erosion rates, given that plants erode continually at the distal end. Erosion rates were calculated using the following formula:

$$\text{Erosion rate (mm per day)} = \frac{(L_2 - H_2) - (L_1 - H_1)}{T}$$

Where  $L_1$  = initial length (mm),  $H_1$  = initial position of hole (mm),  $L_2$  = final length (mm),  $H_2$  = final position of hole (mm),  $T$  = period between measurements (Days).

Plants were then remeasured approximately 1 month later when the tides were low enough. New holes were punched at 50 mm above the blade stipe margin. Dead plants were replaced with new plants. Mortality was measured as the number tagged plants missing or plants with no obvious blade present. It was assumed that tag loss was negligible (see above) so missing plants were assumed to have been ripped from the substrata. Data were analysed using ANCOVA in Statistica 6.0™ using initial length as a covariate. Site was used as a fixed factor. Prior to analysis, data were tested for homogeneity of regression slopes and homogeneity of variances. Appropriate transformations were done as required.

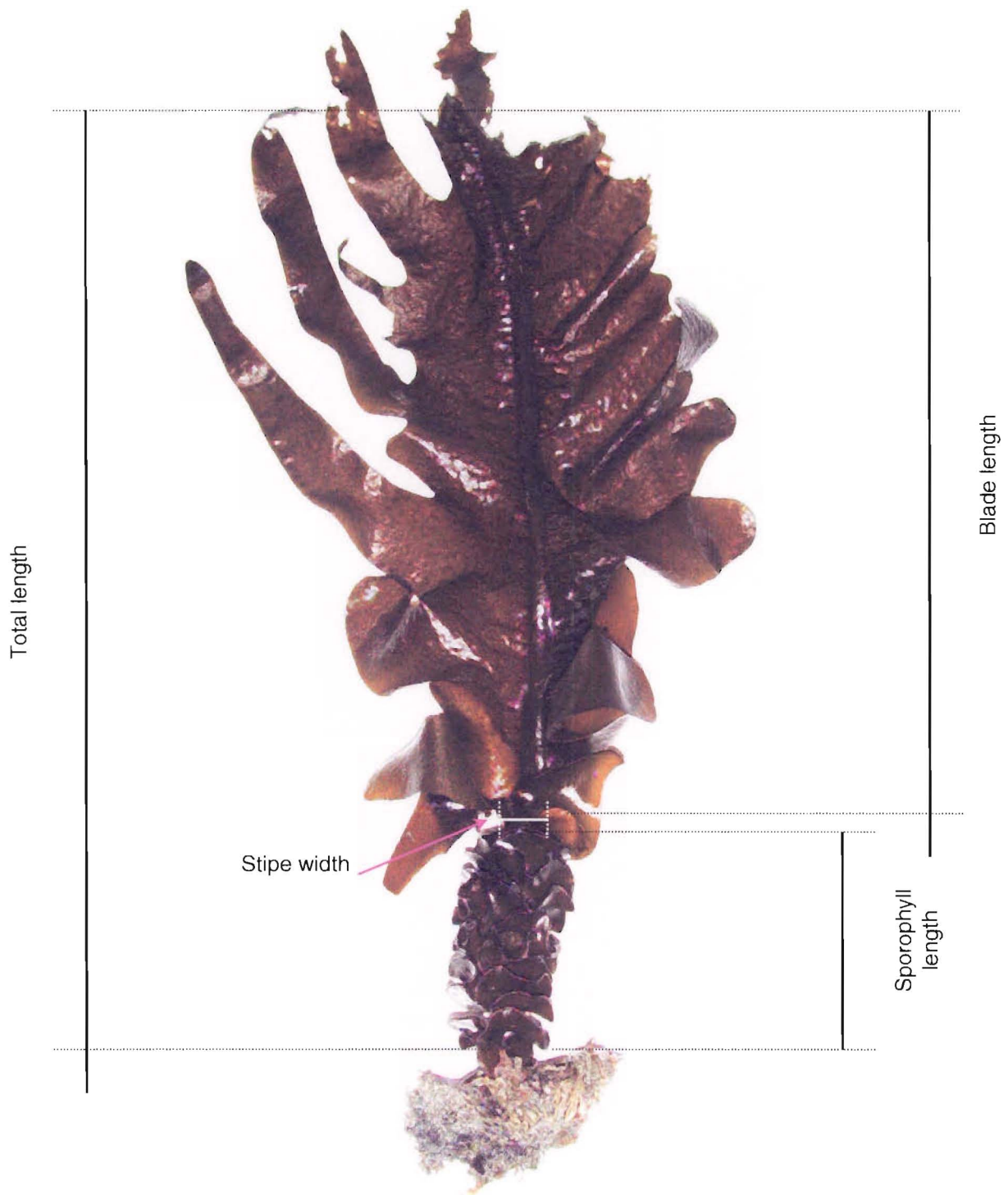


Figure 2.1: Photograph of *U. pinnatifida* showing the measurements taken for plants measured *in situ*.



### 2.2.3 Reproduction

It was noticed early in the study that the presence of a sporophyll did not necessarily indicate that a plant was reproductive. To determine the reproductive periodicity of *U. pinnatifida*, 20 mature plants were collected each month between November 2001 – December 2002 from Diamond Harbour and the Moeraki Platform. Each sporophyll was excised from the plant, wrapped in tissue paper and left to desiccate for two hours in a cool dark area. When sufficiently desiccated the sporophylls were immersed in two litres of filtered seawater and agitated to release spores. Three 1 ml samples of “spore solution” were then pipetted onto a graticule and the number of spores, if present, were counted. If greater than  $1 \times 10^3$  spores per ml were present then the plant was deemed to be reproductive. This was based on Reed's (1990a) previous work on *Macrocystis pyrifera* and *Pterygophora californica*, which showed that 1 spore per mm was needed for successful recruitment. This related to very dilute spore suspensions ( $< 1 \times 10^4$  as  $1 \times 10^4$  per mL produced approximately 180 spore per mm). It was assumed that successful fertilisation would occur for *U. pinnatifida* with spore suspensions of  $1 \times 10^3$  spores per mL.

#### Reproductive output

There were inherent difficulties in trying to determine the reproductive output of *U. pinnatifida*. Several of methods for determining reproductive output were tried but the results proved too inaccurate for a number of reasons. First, it was too difficult to determine the stage of release of the sporophyll. Sporophylls that appeared to be in an ideal state of release released very few spores, indicating that they had either released or were not ready to. Furthermore, it was noticed that some areas of the sporophyll would release whereas others would not. To combat these problems it was decided to get an estimate of the potential reproductive output by counting the number of sporangia per plant (see Chapman 1984). As 32 spores are present in each sporangium an estimate of total spore production can be given.

To estimate the total potential reproductive output of individual sporophylls the length-area relationship was calculated. To do this 15 mature plants of varying length were collected from the Diamond Harbour and Rapaki Bay sites. The sporophylls were then excised from the plant. To determine the volume-area relationship volume

displacement was used. To do this 1 x 1, 2 x 2, 3 x 3 and 4 x 4 cm samples were excised from 6 randomly chosen sporophylls and placed in a 20 mL measuring cylinder. The volume displacement was measured. Next 50 mature plants with varying sporophyll length were randomly collected from each of the four sites and the Moeraki Platform mid zone during spring 2002. Reproductive tissue from the sporophylls was excised from the plants and placed in a 500 mL beaker and the volume displacement measured. The volume displacement was plotted against length of the sporophyll to produce an equation of the relationship between length and volume. These equations were used to calculate the total volume of the sporophyll. The final estimate involved calculating the number of sporangia present in one mm<sup>2</sup> of sporophyll tissue. Thin slivers of sporophyll were excised from ten randomly chosen plants collected during October 2002. Samples were taken near the sporophyll margin and close to the stipe from top, middle and bottom of the sporophyll and examined under a microscope at 400 X magnification. Number of sporangia were counted within a 1 mm<sup>2</sup> area.

#### **2.2.4 Spore Dispersal**

To estimate accurately the ability of spores to disperse, an experiment was done within the intertidal zone at Moeraki Platform during October 2002. The experiment was carried out on calm days and was set up in tide pools scattered within the platform. Tidepools were denuded of sporophytes the previous day. Wave force was measured during the experiment using three dynamometers (*c.f.* Bell and Denny 1994) placed within the experimental areas. Wave force never exceeded 2 Nm.

To test the hypothesis that spore dispersal would decrease further away from the parent source four arrays of microscope slides were set out within large tidepools during low tide. Slides were arranged in four rows radiating at right angles from the sporophyll source. The microscope slides making up each array were attached to a rope and positioned beneath the parent plant at distances of 2, 5, 10, 20, 40, 80, and 160 cm from it. The rope was held down by lead weights. Series of slides were positioned so that they (a) faced land and were parallel with incoming waves (landward), (b) faced the sea and were parallel to incoming waves (seaward), and (c) were perpendicular to the incoming waves (left and right).

Twelve mature sporophylls of similar volume were collected from the low shore, rinsed, wrapped in damp paper and desiccated for 2 hours in the shade to induce spore release. Three sporophylls were then placed into each of 4 nylon mesh bags and weighed down with lead weights at the centre of their respective pools. The experiment began on the incoming tide and continued to run until the next outgoing tide (a period of approximately 6 hours). The experiment was run during daylight as spores are not released during the hours of darkness (Saito 1975).

After completion of the experiment microscope slides were carefully removed and transported back to the laboratory. Spores were counted under a microscope. The small size of spores (5- 6  $\mu\text{m}$ ) and their large numbers necessitated sub sampling of the slides. Spore abundance was estimated as numbers per  $\text{mm}^2$ . Three-way ANOVA was performed on the data using Statistica 6.0™. Prior to analysis, data were tested for homogeneity of variances using Cochran's test. Data did not need transforming.

### **2.2.5 Recruitment**

Recruitment was monitored monthly between June 2000 and May 2002 following the methods in Section 2.2.1.

In order to monitor recruit survival replicate 0.25  $\text{cm}^2$  permanent quadrats were placed within areas that had newly recruited *U. pinnatifida*. This was done during April/May 2001 and August/September 2001 at Diamond Harbour and Moeraki Platform. Quadrats were identified by marking three corners with plumbing tape anchored to the substrata with nylon Ramset® bolts. Individual plants were then mapped and measured for total length, stipe length and stipe width. The time at which maturity was reached (the presence of a sporophyll) was also noted. When the plants became large enough they were tagged. Enough quadrats were used to ensure a large enough number of recruits could be used (i.e. at least 10).

## 2.3 Results

### 2.3.1 Population Structure

#### *Abundance*

The abundance of *Undaria pinnatifida* in the low tidal zone of each of the four sites showed a distinct annual cycle (Fig. 2.2) with greatest abundance occurring between late autumn- spring (April- September) and lowest abundance occurring during the early summer- early autumn period (December- March). Greatest abundance was associated with periods of intense recruitment whereas the decline in abundance during the summer was due to the lack of recruitment and the onset of senescence in post-reproductive mature plants.

Plants could be found during all months of the sampling period at the Moeraki sites. In contrast, *U. pinnatifida* was absent from the Lyttelton Harbour sites for part of the summer. At Diamond Harbour a small hiatus was observed during February 2001, but at Rapaki Bay the length of the hiatus was considerably longer lasting from December 2000 until April 2001. This was followed by a smaller period of absence the following summer during February and March 2002. The occurrence of these periods during the summer months seemed to have no effect on subsequent peaks in abundance. For example, the Diamond Harbour site had the greatest abundance of all sites during autumn 2001, only 2 months after no macroscopic plants were found. Although, timing of peak abundance was highly variable the density of peak abundance was not significantly different between each of the four sites (Table 2.1).

#### *Size Structure*

Contrasting patterns of size structure and plant development occurred at the four sites (Fig. 2.3). Significant differences in maximal plant length occurred among all sites (Table 2.1). Maximal length was greatest at the Moeraki Platform whereas maximal plant length at Diamond Harbour was the smallest (Table 2.1). During May 2001 there was a period of intense recruitment at all four sites. By August 2001 some of the new recruits had developed into mature plants. Recruitment occurred sporadically during most of 2001 at all sites (see Appendix I) but at the two Lyttelton Harbour sites a large pulse occurred during August 2001. The sporadic recruitment

that occurred later in the year at all sites meant that during periods when mature plants were most abundant immature plants could also be found. The most notable difference was the presence of plants at the Moeraki sites during February 2001, a period when no plants were found at the Lyttelton Harbour sites.

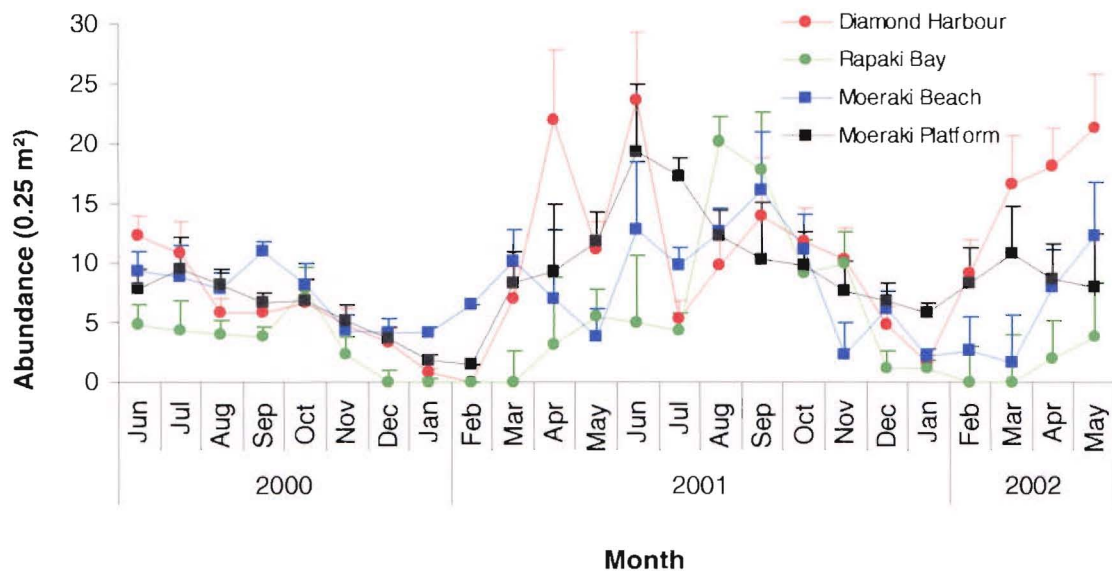


Figure 2.2: Mean abundance of *U. pinnatifida* (plants per 0.25 m<sup>2</sup> ± 1 S.E.) at Diamond Harbour, Rapaki Bay, Moeraki Beach and Moeraki Platform between June 2000 and May 2002. n=10 samples each month.

Table 2.1: Mean maximal size and density (± 1 S.E.) of *U. pinnatifida* in the low zone at each site during the period between June 2000 and May 2002. ANOVA (one way) results are given in the right hand column (a,b,c indicate results of Tukey's HSD test; sites with the same letter were not significantly different at p<0.05). Data were log-transformed. Cochran's test was not significant.

Peak Measurement	Diamond Harbour	Rapaki Bay	Moeraki Beach	Moeraki Platform	ANOVA results
Total length (mm)	418.7 ± 27.2 a	503.4 ± 39.7 b	500 ± 44.64 b	898.6 ± 58.4 c	$F_{(3,196)} = 16.29$ $p < 0.001^{**}$
Density (plants/0.25m <sup>2</sup> )	23.6 ± 5.7 a	20.2 ± 2.5 a	16.1 ± 1.74 a	19.3 ± 3.74 a	$F_{(3,36)} = 0.58$ $p = 0.62$

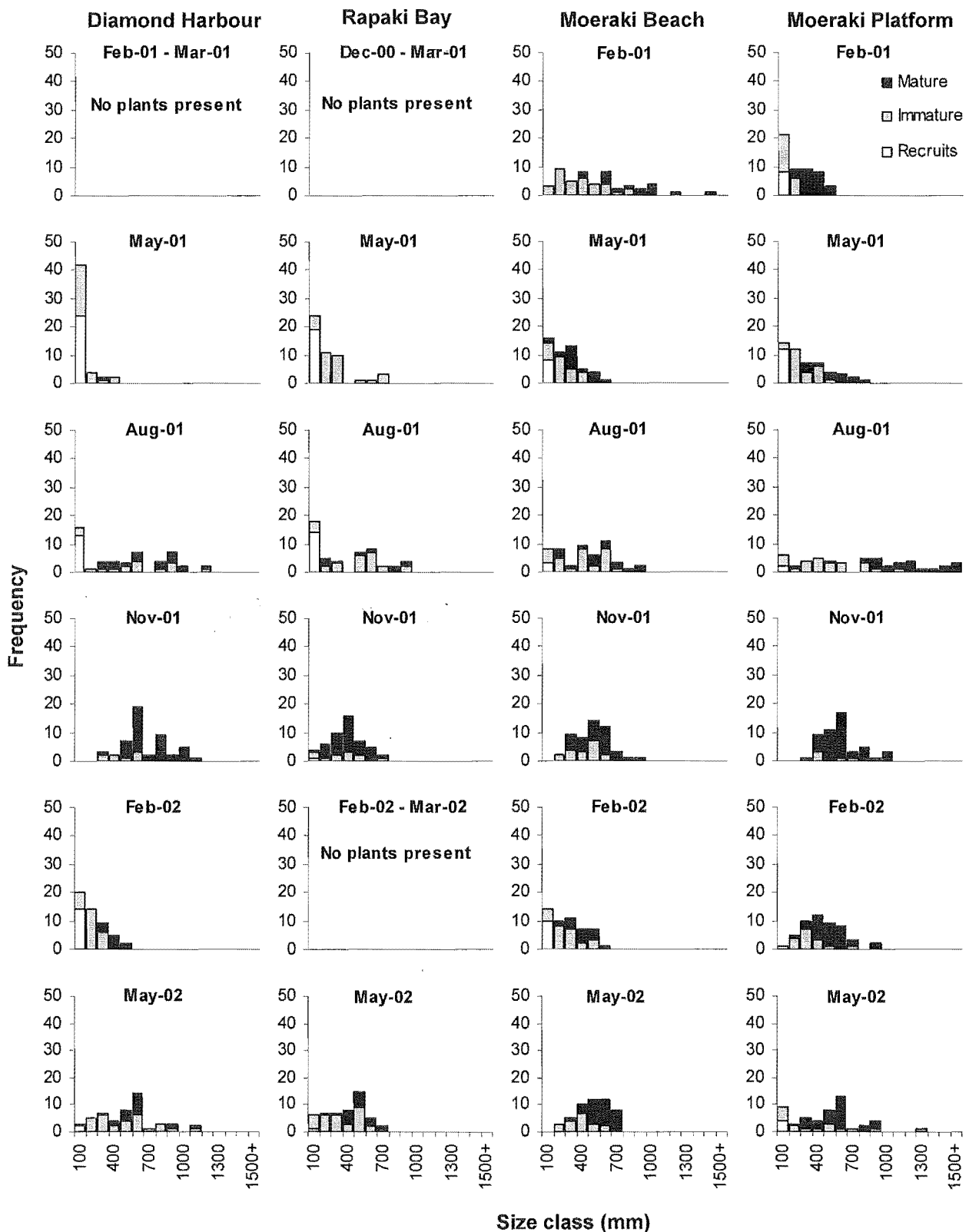


Figure 2.3: Size-frequency histograms of recruit, immature and mature *U. pinnatifida* plants from the low zone at Diamond Harbour, Rapaki Bay, the Moeraki Platform and Moeraki Beach between February 2001 and May 2002 at quarterly intervals.  $n=50$  plants each month. Shaded bars are stacked.

With the exception of the Moeraki Platform few plants exceeded 700 mm (Fig. 2.3). The largest plants were found at Moeraki Platform during August 2001 with some individuals greater than 1500 mm in length. Maximal length of plants occurred during winter when growth was greatest. During the late spring (November) the larger size classes began to disappear. This was the result of senescence in mature plants and the tips of large immature plants dying off during periods of exposure at low tide.

At Moeraki, mature plants occurred during all months and were most prevalent from November 2001 to February 2002. Although mature plants were found later at the Lyttelton Harbour sites, they were also most prevalent from late spring to early summer. By mid summer the majority of plants were post-reproductive and senescing (mature plants that occupied smaller size classes) (Appendix I). Although the majority of mature plants began to senesce around November/December 2001 small numbers of senescing plants could be found during most months of the year. Senescence in old mature plants was characterised by a discolouration at the tip of the blade from a golden-brown colour to a pale brown colour. This was followed by degeneration of the blade until all that was left was the pale brown spent sporophyll which typically rotted within a month.

#### *Moeraki Platform zones*

There were distinct differences in plant abundance within the different zones at Moeraki Platform. Plants were present throughout the entire sampling period within the low zone but were absent from the mid zone during March 2001 and January-February 2002 (Fig. 2.4). Plants were only present in the upper mid zone between the late autumn and winter months. Peak abundance occurred during the autumn months for all zones when most recruits appeared. Far fewer plants recruited into the upper mid zone (Table 2.2). There were no macroscopic plants in the mid and upper mid zones during February 2001, and for much longer periods in the upper mid zone. For much of the study fewer plants occurred in the low zone than in the mid zone (Table 2.2).

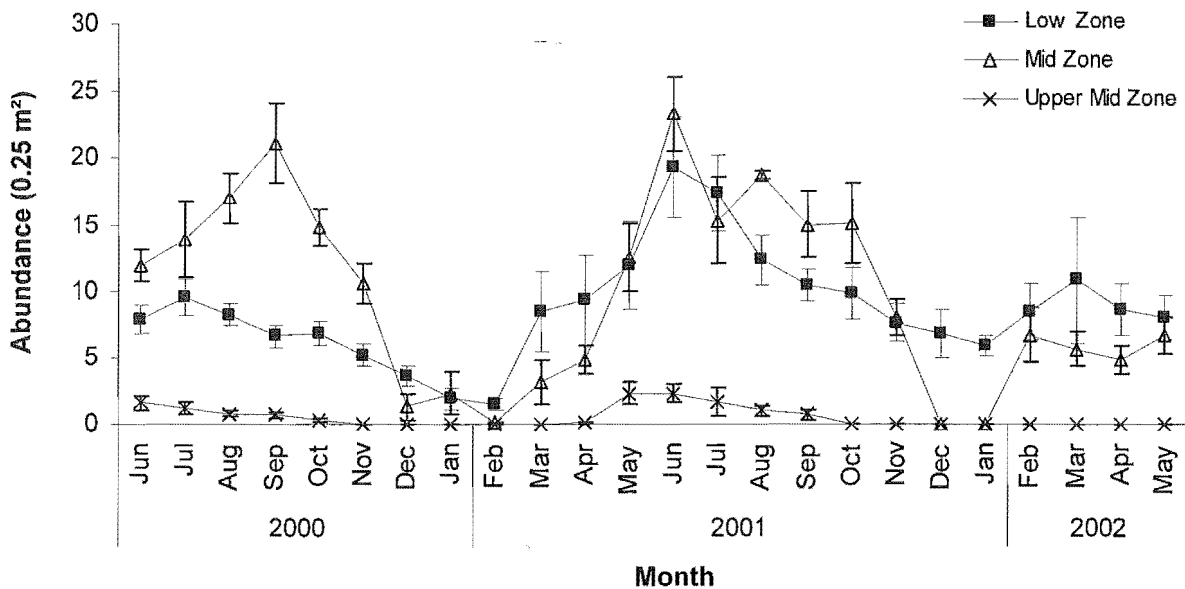


Figure 2.4: Mean abundance of *U. pinnatifida* (plants per 0.25 m<sup>2</sup> ± 1 S.E.) at the low, mid and upper mid zone of Moeraki Platform between June 2000 and May 2002. n=10 samples each month.

Table 2.2: Mean maximal size and density (± 1 S.E.) of *U. pinnatifida* in the low mid and upper mid zones at Moeraki Platform. ANOVA (one way) results are given in the right hand column (a,b,c indicate results of Tukey's HSD test; sites with the same letter were not significantly different at p<0.05). Data were log transformed. Cochran's test was not significant.

Peak Measurement	Low zone	Mid zone	Upper Mid zone	ANOVA results
Total length (mm)	564.2 ± 77.9 a	374 ± 33.7 b	187.4 ± 15.0 c	$F_{(2,147)} = 72.12$ $p < 0.001^{**}$
Peak density (plants/ 0.25 m <sup>2</sup> )	19.3 ± 3.74 a	18.7 ± 0.33 a	2.3 ± 0.86 b	$F_{(2,27)} = 20.88$ $p < 0.001^{**}$

Significant differences in maximal plant length occurred between the zones (Table 2.2), with a gradient in sizes from the upper mid to low zones. The largest plants reached 1900 mm in length in the low zone but rarely reached sizes > 300 mm in the upper mid zone.

Although large numbers of recruits were found in the upper mid zone over a short period (May 2001- August 2001), the low number of immature plants and lack of mature plants found in subsequent months indicate 100% mortality (Fig. 2.5). In contrast, extended periods of recruitment occurred in the mid and low zones from late summer until early spring. Survival of recruits appeared to be greater in the low



and mid zones as large numbers of immature plants were found following periods of recruitment. Although similar patterns of plant development occurred in the low and mid zones, larger size classes of mature plants were found in the low zone during all months of sampling. The largest plants were found in the low zone in August 2001 (Fig. 2.5).

### **2.3.2 Growth**

Similar temporal trends occurred at all sites and zones with maximal growth occurring over the winter- spring months (June- October) and lowest growth occurring during the summer months (Fig. 2.6a). Erosion rates were greatest after periods of peak growth and typically occurred during late winter (Fig 2.6b). Although similar temporal patterns growth and erosion occurred they were highly variable between sites (Fig. 2.6a and Fig. 2.6b). Immediately after periods of high growth, plant length was at its maximum (Fig. 2.6a and 2.6c). This was followed by periods of maximum erosion, which had an overall effect of reducing total plant length (Fig. 2.6b and 2.6c). By summer, erosion rates had declined, but because of very low growth rates during this period meant plant length was at its lowest at all sites.

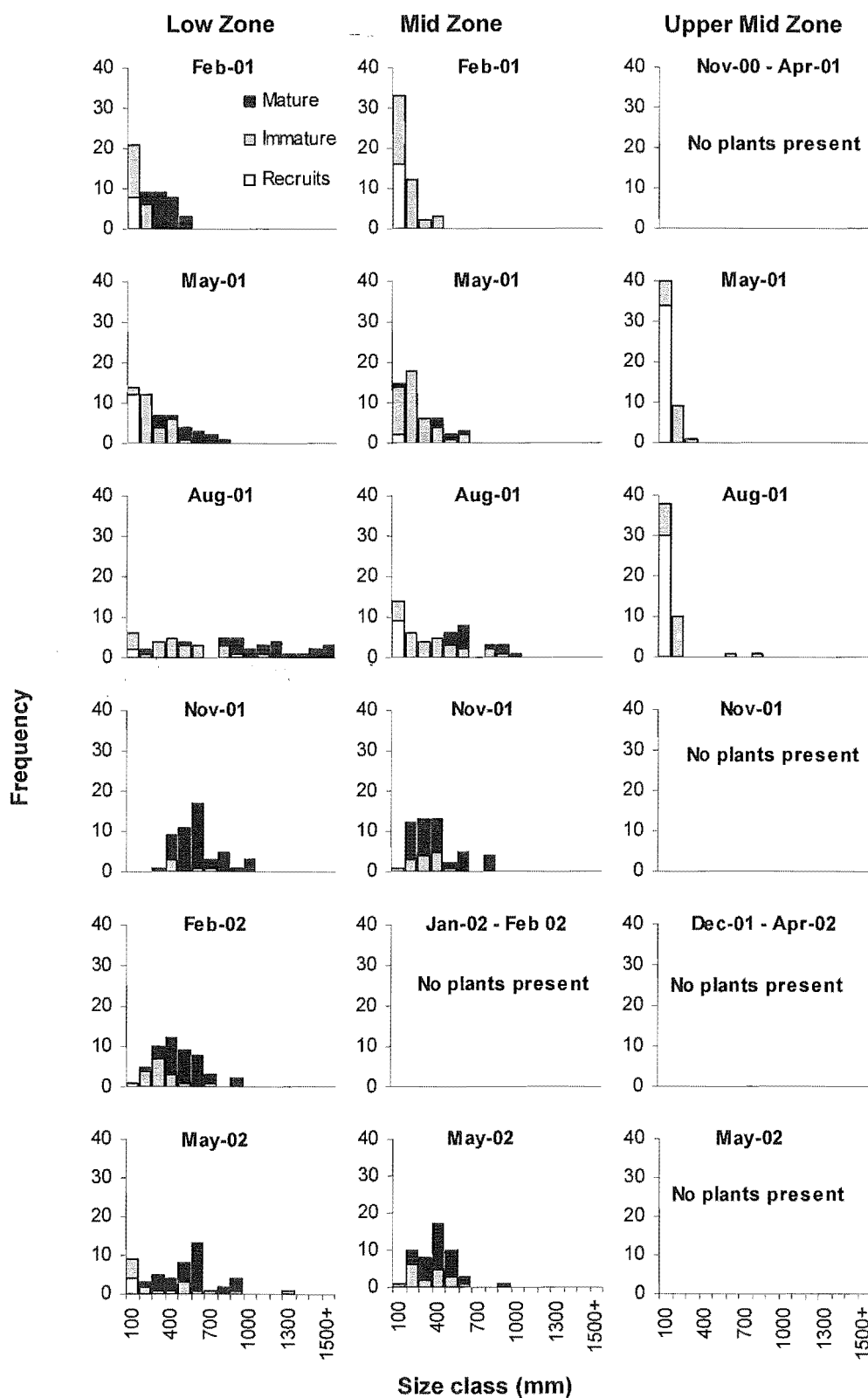


Figure 2.5: Size-frequency histograms of recruit, immature and mature *U. pinnaefida* plants from the low zone, mid zone and upper mid zone of Moeraki Platform between February 2001 and May 2002 at quarterly intervals.  $n=50$  plants each month. Shaded bars are stacked.

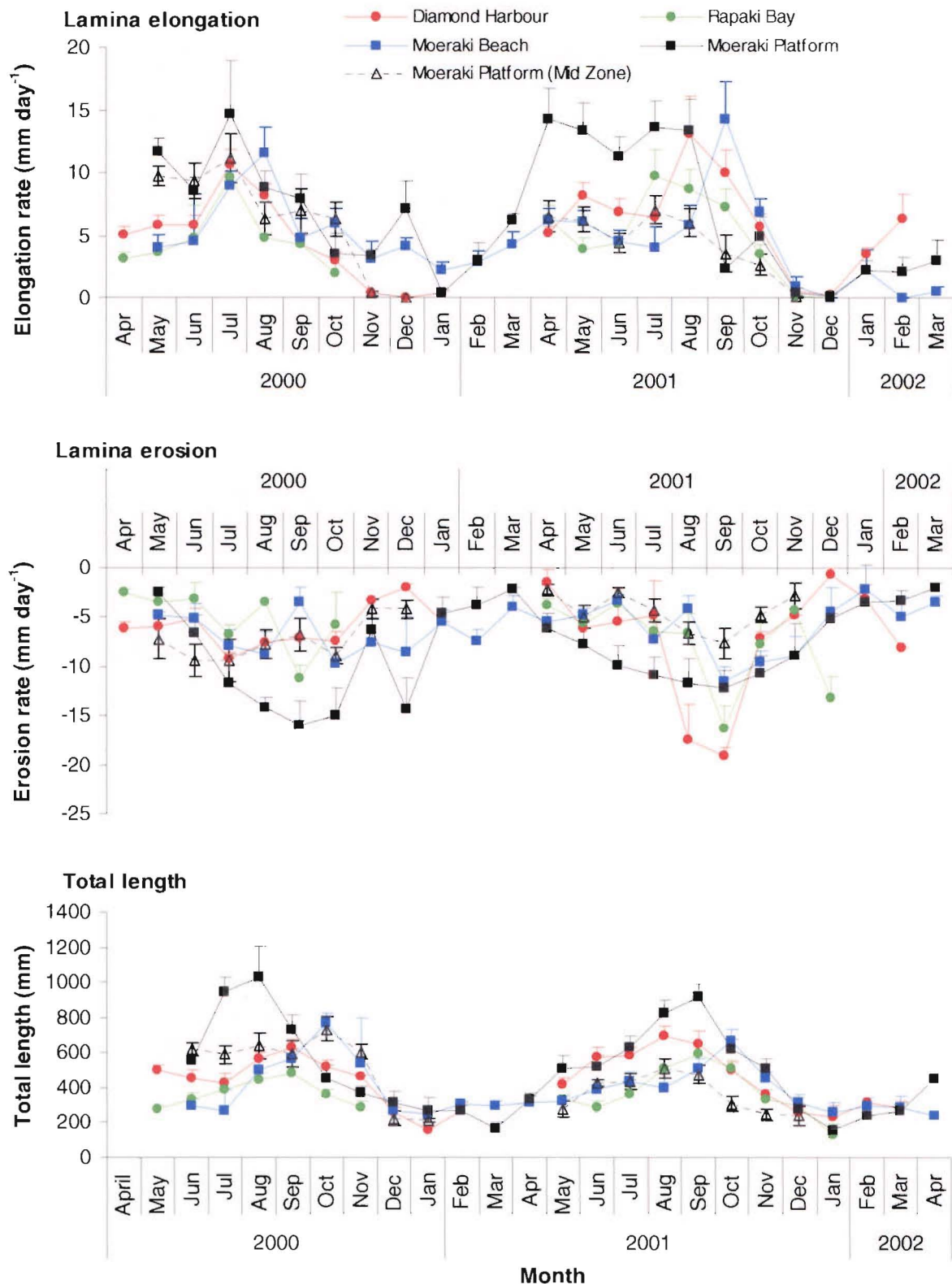


Figure 2.6: Mean growth measurements ( $\pm 1$  S.E.) of *U. pinnatifida* taken between April 2000 and April 2002 at Diamond Harbour, Rapaki Bay, Moeraki Beach, Moeraki Platform and Moeraki Platform mid zone.

To assess differences in elongation and erosion rates between sites ANCOVA was used with initial plant length used as a covariate. Elongation rates were significantly related to initial plant size during both years (Table 2.3 and 2.4). Peak elongation rates differed significantly between sites during 2000 but not during 2001 (Table 2.3, 2.4 and 2.5). The significant site effect observed during 2000 was due lower peak elongation rates of plants at Rapaki Bay (Table 2.5).

**Table 2.3. Results of one way ANCOVA performed on the maximum elongation rates of *U. pinnatifida* at Diamond Harbour, Rapaki Bay, Moeraki Beach and Moeraki Platform during 2000. Elongation rates were estimated by hole punch method. Initial size was used as a covariate. \*\* is significant at  $p < 0.01$ , \* is significant at  $p < 0.05$ . Data were log-transformed. Cochran's test was not significant. Test for homogeneity of slopes was not significant.**

Effect	df	MS	F	p-level
Initial length	1	4.160	32.295	$p < 0.01^{**}$
Site	3	0.386	3.00	0.032*
Error	154	0.128		

**Table 2.4. Results of one way ANCOVA performed on the maximum elongation rates of *U. pinnatifida* at Diamond Harbour, Rapaki Bay, Moeraki Beach and Moeraki Platform during 2001. Elongation rates were estimated by hole punch method Initial size was used as a covariate. \*\* is significant at  $p < 0.01$ . Data were log-transformed. Cochran's test was not significant. Test for homogeneity of slopes was not significant.**

Effect	df	MS	F	p-level
Initial length	1	2.82	21.01	$p < 0.01^{**}$
Site	3	0.150	1.118	0.343
Error	178	0.134		

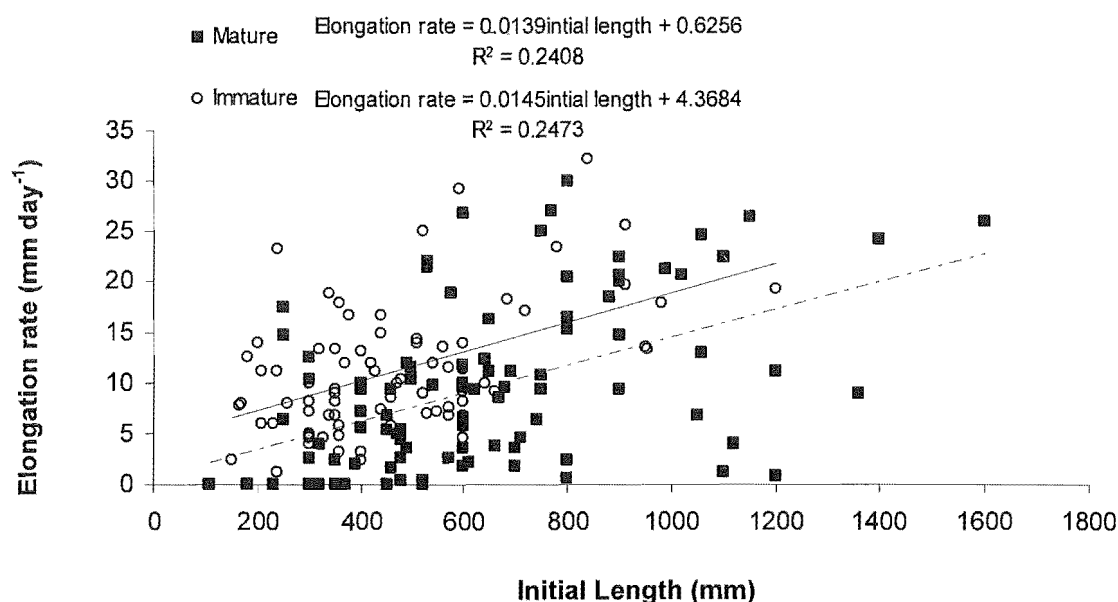
**Table 2.5: Mean maximal elongation rates ( $\pm 1$  s.e.) of *U. pinnatifida* in the low zone at each site during 2000 and 2001. ANOVA (one way) results are given in the right hand column (a,b indicate results of Tukey's HSD test; sites with the same letter were not significantly different at  $p < 0.05$ ). Data were log-transformed. Cochran's test was not significant.**

Elongation (mm day <sup>-1</sup> )	Diamond Harbour	Rapaki Bay	Moeraki Beach	Moeraki Platform
2000	8.35 $\pm$ 0.65 a	5.5 $\pm$ 0.47 b	9.74 $\pm$ 1.07a	9.3 $\pm$ 1.18 a
2001	9.96 $\pm$ 1.04 a	8.62 $\pm$ 1.03 a	9.08 $\pm$ 1.2 a	12.8 $\pm$ 1.19 a

To assess whether the reproductive stage of plants affected growth, data collected from peak growth periods during 2001 were separated into mature and immature stages (the data from 2000 were omitted due to low numbers of immature plants at Moeraki Beach and Moeraki Platform sites). Although there was considerable scatter, the results of ANCOVA showed that as well as initial size, the stage of the plant had a significant effect on elongation rates (Table 2.6). For a given length, immature plants grew at a greater rate than mature plants. As there were no differences in elongation rates between sites the data presented in Figure 2.7 are pooled to show the patterns of growth for the two stages.

**Table 2.6: Results of two-way ANCOVA on elongation rates of immature and mature *U. pinnatifida* plants May 2001 and October 2001. Initial length was the covariate. Stage (=mature, immature), site(=at Diamond Harbour, Rapaki Bay, Moeraki Beach and Moeraki Platform). \*\* is significant at  $p < 0.01$ . Data were log-transformed. Cochran's test was not significant. Test for homogeneity of slopes was not significant.**

Effect	df	MS	F	p-level
Initial length	1	3.579	34.82	$p < 0.01^{**}$
Stage	1	3.129	30.45	$p < 0.01^{**}$
Site	3	0.177	1.725	0.164
Stage x Site	3	0.176	1.7135	0.166
Error	166	0.1028		



**Figure 2.7:** Scatterplot of initial length versus elongation rates for immature and mature *U. pinnatifida* plants measured between May 2001 and October 2001. Elongation rates were estimated by hole punch method. Dashed line = mature; solid line = immature. The data are pooled across sites.

Erosion rates were significantly related to initial plant length during 2000 and 2001 with larger plants eroding more (Fig. 2.8). There were significant differences in erosion rates between the sites during 2000 but not 2001 (Table 2.7 and 2.8). The differences observed during 2000 were due to the higher erosion rates observed at the Moeraki Platform site and the lower erosion rates observed at Rapaki Bay (Table 2.8). During 2001 Diamond Harbour and the Moeraki Platform had higher erosion rates than the Rapaki Bay and Moeraki Beach sites. Erosion rates were also closely related to maximum plant length at all sites (Fig. 2.9). Although wave exposure was not measured during the experiment the Moeraki sites generally had greater wave action than the Lyttelton Harbour sites.

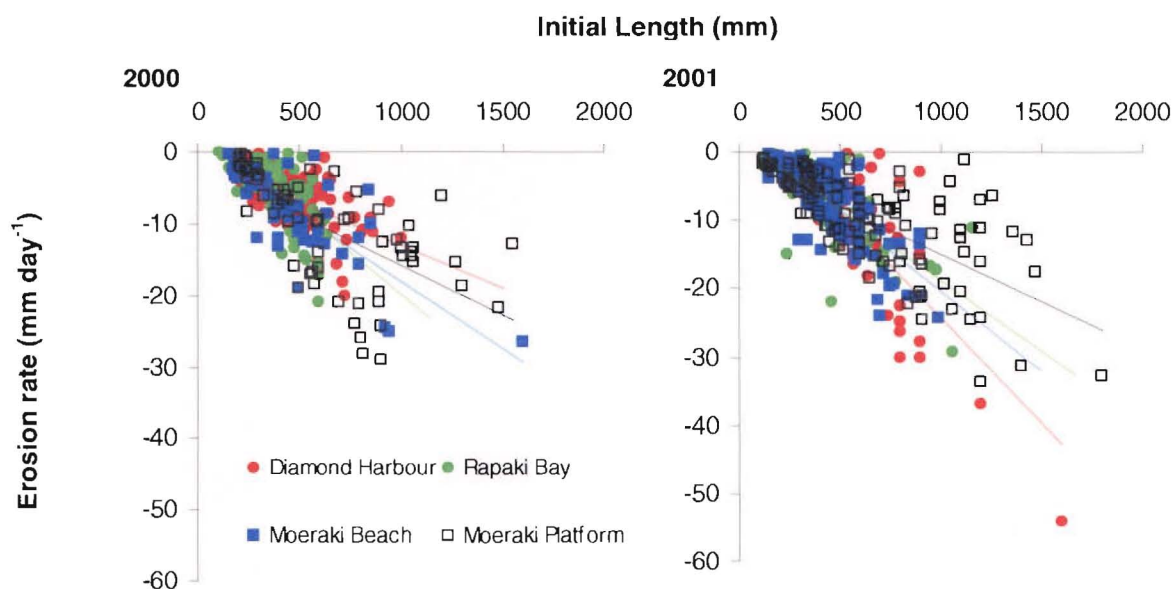


Figure 2.8: Erosion rates ( $\text{mm day}^{-1}$ ) of *U. pinnatifida* at Diamond Harbour, Rapaki Bay, Moeraki Beach and Moeraki Platform between 2000 and 2001.

Table 2.7. Results of one-way ANCOVA on erosion rates of *U. pinnatifida* 2000 (June-December) and 2001 (January-December) at Diamond Harbour, Rapaki Bay, Moeraki Beach and Moeraki Platform. Initial size was used as a covariate. \*\* is significant at  $p < 0.01$ , \* is significant at  $p < 0.05$ . Data were log-transformed. Cochran's test was not significant. Test for homogeneity of slopes was not significant.

Year	Effect	df	MS	F	p-level
2000	Initial length	1	0.095	258.37	$p < 0.001^{**}$
	Site	3	0.001	3.8	0.011*
	Error	357	0.0004		
2001	Initial length	1	0.23	366.94	$p < 0.001^{**}$
	Site	3	0.0006	0.94	0.422
	Error	449	0.0006		

Table 2.8: Mean erosion rates ( $\pm 1$  S.E.) of *U. pinnatifida* during 2000 (June-December) and 2001 (January-December). (a,b,c, indicate results of Tukey's HSD test; sites with the same letter were not significantly different at  $p < 0.05$ ). Data were log-transformed. Cochran's test was not significant. Test for homogeneity of slopes was not significant.

Erosion rate ( $\text{mm day}^{-1}$ )	Diamond Harbour	Rapaki Bay	Moeraki Beach	Moeraki Platform
2000	$-6.64 \pm 0.32$ a	$-5.06 \pm 0.46$ b	$-7.43 \pm 0.65$ a	$-10.59 \pm 0.95$ c
2001	$-9.03 \pm 1.02$ a	$-6.53 \pm 0.57$ b	$-6.64 \pm 0.39$ b	$-9.58 \pm 0.64$ a

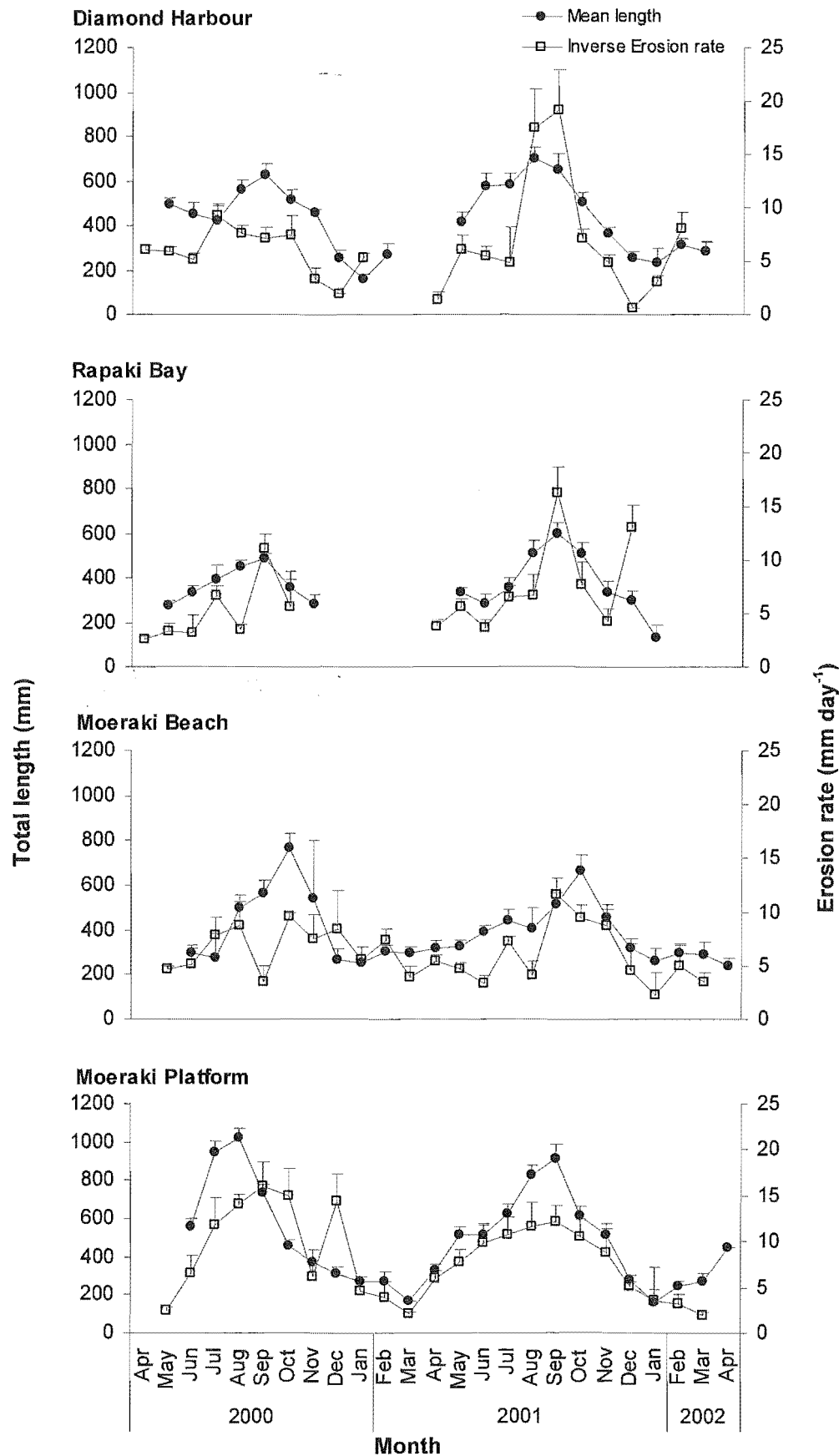


Figure 2.9: Mean inverse erosion rates (mm day<sup>-1</sup>) vs mean plant length of *U. pinnatifida* at Diamond Harbour, Rapaki Bay, Moeraki Beach and Moeraki Platform between April 2000 and April 2002. (+1 s.e.).



### 2.3.3 Reproduction

There were similar patterns of spore release for mature plants between November 2000 and November 2001 at all four sites and the mid shore zone of the Moeraki Platform (Fig. 2.10). During the summer of 2000/01 most plants were fertile at Diamond Harbour, Moeraki Beach and Moeraki Platform (Fig. 2.10). Reproduction occurred at the Moeraki sites during the summer months of 2001. In contrast, at Rapaki Bay large numbers of fertile plants were found in November 2000 after which no plants could be found. In autumn 2001, although mature plants (i.e. those bearing sporophylls, see Fig. 2.3) were present in the population they were not fertile. The first fertile plants of the new 2001 cohort were found in small numbers between June and July 2001 at all sites. A gradual increase in the number of fertile plants was observed during August. This culminated in the majority of mature plants becoming fertile between September and November.

The number of sporangia per mm<sup>2</sup> was similar across all size classes and sites used ( $F_{(df\ 2,72)}=0.176$ ,  $p=0.839$ ). The mean number of sporangia per mm<sup>2</sup> across all sites was  $375.53 \pm 6.92$ . This corresponded to approximately 900,000 spores per cm<sup>2</sup> of tissue. Mean sporophyll length differed significantly among the sites ( $F_{(df\ 3,1935)}=18.46$ ,  $p<0.0001$ ) with the Diamond Harbour and Moeraki Platform sites having the longest sporophylls (Table 2.9). Furthermore, the low zone at Moeraki Platform had significantly longer sporophylls than the mid zone ( $F_{(df\ 1,1006)}=26.04$ ,  $p<0.0001$ ). No plants in the upper mid zone survived to maturity.

Although the sporophylls of Diamond Harbour and Moeraki Platform plants were similar in length their overall potential spore production (assuming the presence of sporophylls were indicative of eventual spore release) was significantly different (Table 2.9). This was due to the larger volumes of the sporophylls at Moeraki Platform. At Moeraki Platform the average sized sporophyll was calculated to produce at least 1 billion spores whereas at Diamond Harbour the average sized sporophyll could potentially produce 673 million spores (Table 2.9). Although Rapaki Bay and Moeraki Beach average sporophyll length did not differ significantly, there were differences in the number of spores produced. The average sized sporophyll at Moeraki Beach was calculated to produce approximately 200 million more spores

than sporophylls at Rapaki Bay (Table 2.9). These differences can be attributed to the larger sporophyll volume at Moeraki Beach (Table 2.9). Mature plants within the mid zone of Moeraki Platform were found to have less than 600 million spores per average sized sporophyll (Table 2.9).

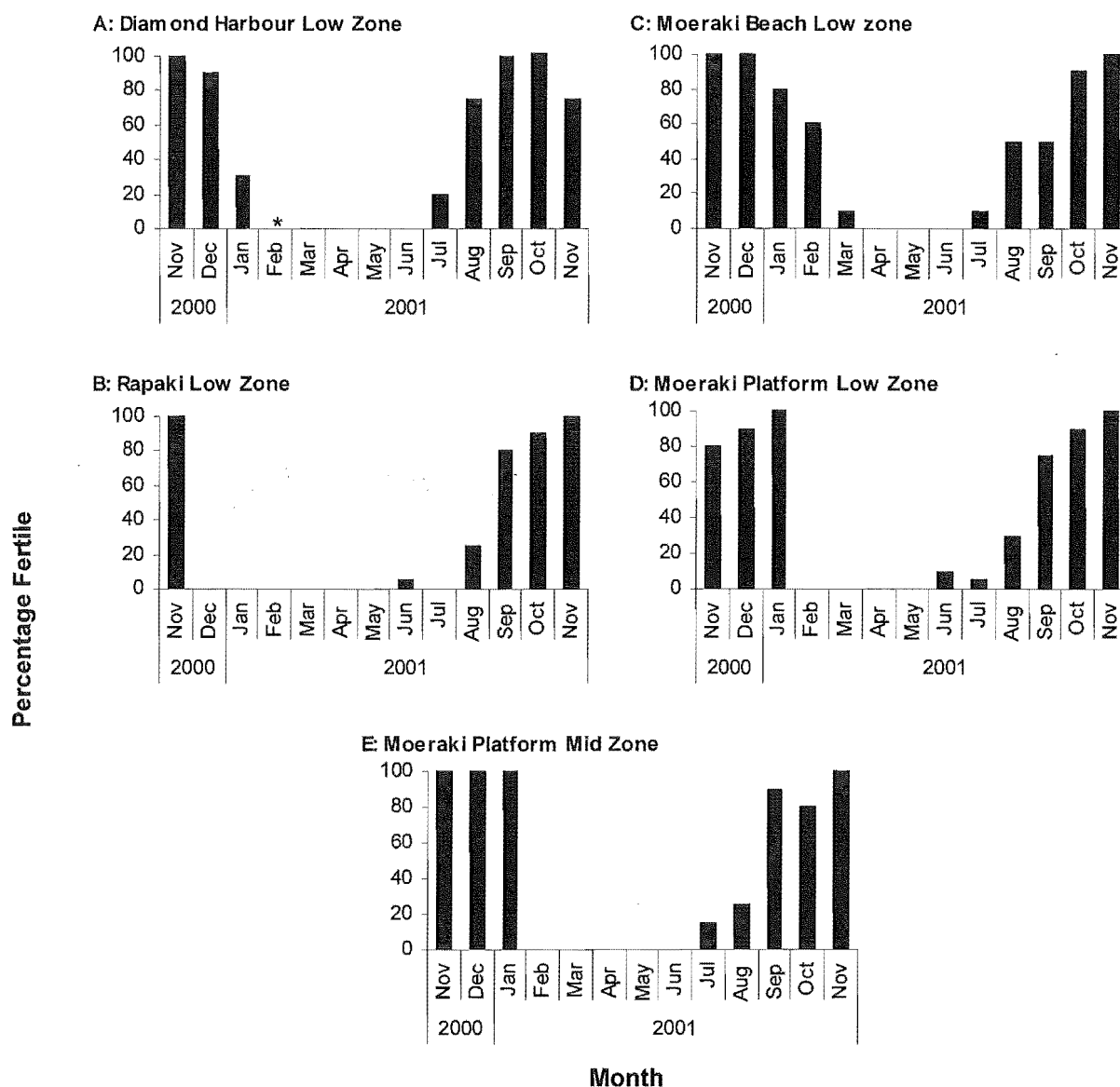


Figure 2.10: Percentage of *U. pinnatifida* population composed of fertile plants at Diamond Harbour, Rapaki Bay, Moeraki Beach, Moeraki Platform and the mid zone of Moeraki Platform between November 2000 and November 2001. n=20.

Table 2.9: Estimates of maximal spore production of mature *U. pinnatifida* at each of the sites and the mid zone of Moeraki platform. Mean sporophyll length is calculated from all sporophylls measured between June 2000 and May 2002. Data were log-transformed. Cochran's test was not significant. Equations represent the volume (ml) to length relationship of *U. pinnatifida* plants. a,b,c indicate results of Tukey's HSD test; sites with the same letter were not significantly different at  $p < 0.05$ ).

Site	Equation of length vs volume	Mean Volume (ml) ± 1 S.E.	Mean sporophyll length (mm) ± 1 S.E.	Number of spores per plant ( $\times 10^6$ )
Diamond Harbour	$y = 1.322x - 58.053$ ( $r^2$ 0.82)	89.10 ± 3.21 a	100.51 ± 2.41 a	673
Rapaki Bay	$y = 0.9063x + 6.878$ ( $r^2$ 0.72)	89.04 ± 3.11 a	89.7 ± 3.49 b	793
Moeraki Beach	$y = 0.8842x + 37.139$ ( $r^2$ 0.92)	44.55 ± 1.71 b	79.07 ± 1.88 b	963
Moeraki Platform	$y = 1.8405x - 65.872$ ( $r^2$ 0.81)	136.06 ± 4.94 c	102.79 ± 2.62 a	1,110
Moeraki Platform (Mid Zone)	$y = 0.8658x - 6.420$ ( $r^2$ 0.91)	65.72 ± 2.43	83.33 ± 2.81	592

### 2.3.4 Spore dispersal

High numbers of spores were released within 5 cm of the parent plant during both days of the experiment (Fig. 2.11). Although the day in which the experiment was run had a significant effect, there was a significant second order interaction between day and direction (Table 2.10). This was the result of slides on the right side treatments having higher numbers of spores settling on the second day than on the first day (Fig. 2.11). For the other three treatments higher numbers of spores settled on the first day than on the second. Although significantly more spores settled close to the parent plant there was a significant second order interaction between distance and direction (Table 2.10). This was due to the high number of spores settling on the landward facing slides and the low numbers settling perpendicular to the incoming waves (Fig. 2.11).

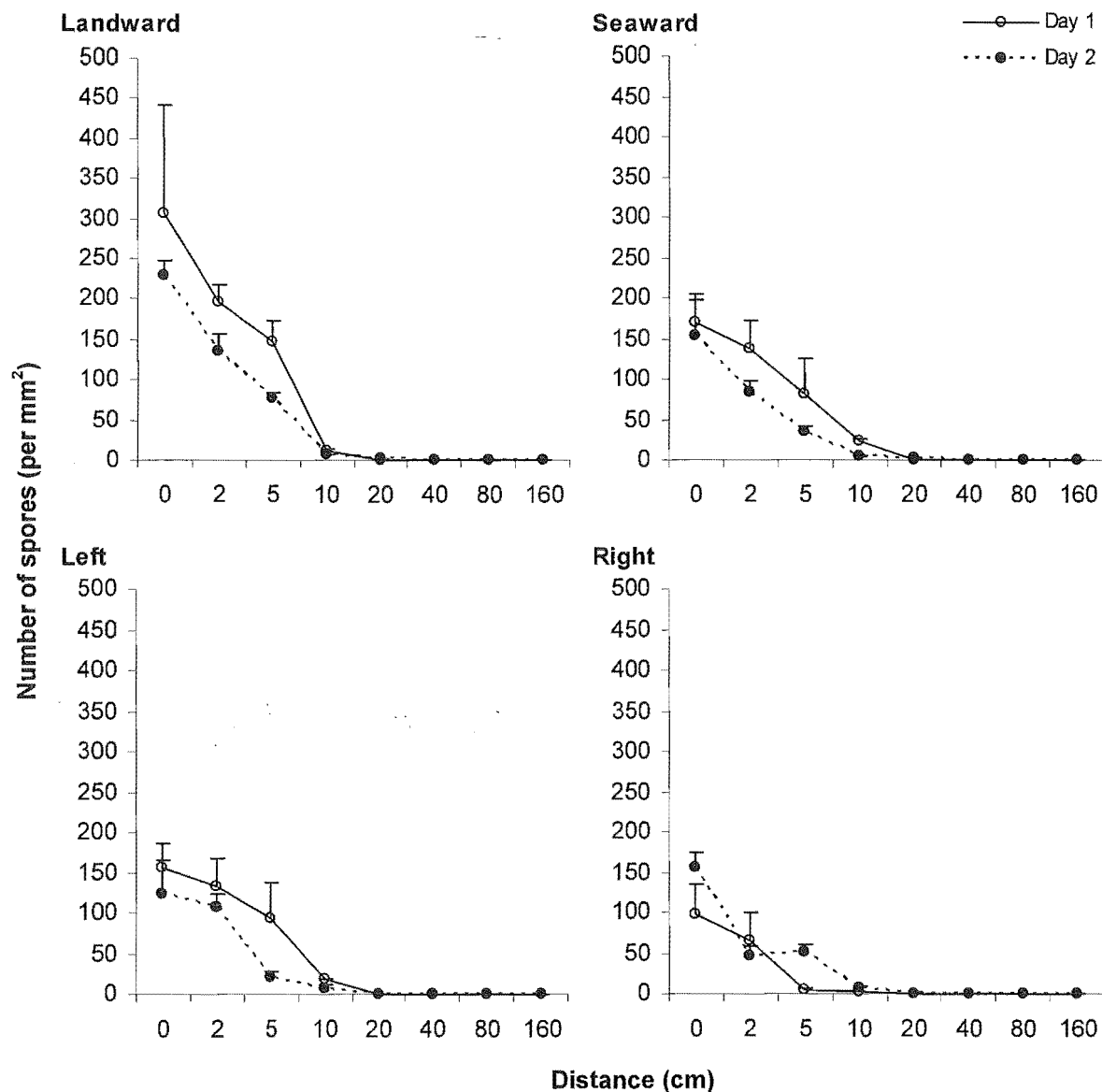


Figure 2.11: Mean number (+1 s.e.) *U. pinnatifida* spores settling onto microscope slides at Moeraki Platform during October 2002. Landward = facing land; Seaward = facing incoming waves, Left = perpendicular to waves (left side facing landward); Right = perpendicular to waves (right side facing landward).

Table 2.10: Results of three-way ANOVA of distance (cm) and direction of *U. pinnatifida* spores (per mm<sup>2</sup>) that settled onto microscope slides at Moeraki Platform over two days during October 2002. \*\* is significant at  $p < 0.01$ , \* is significant at  $p < 0.05$ . Data were not transformed. Cochran's test was not significant.

Effect	df	MS	F	p-value
Day	1	57686	6.434	0.011*
Distance	7	847050	94.48	$p < 0.01^{**}$
Direction	3	121252	13.528	$p < 0.01^{**}$
Day x Distance	7	13271	1.481	0.17
Day x Direction	3	25558	2.851	0.036*
Distance x Direction	21	33655	3.754	$p < 0.01^{**}$
Day x Distance x Direction	21	7835	0.874	0.626
Error	1471	8966		

### 2.3.5 Recruitment

#### Low zone

Most *U. pinnatifida* recruits appeared between the autumn and spring seasons (April-October) but their abundance and timing was highly variable (Fig. 2.12). Moeraki Platform consistently had the highest levels of recruitment whereas Rapaki Bay had the lowest levels. During the spring of 2000, small peaks of recruitment occurred at all four sites but did not coincide. The peaks in recruitment occurred during September at the Lyttelton Harbour sites whereas the peaks were observed 1 month later at the Moeraki sites. After the spring recruitment period there was no more recruitment over the summer months at all four sites. Recruits appeared in the following March- April but were highly variable in abundance and timing after this initial appearance. During 2001, there were two periods of high recruitment. These periods occurred during the autumn and spring months at all sites.

Recruitment within the different zones of Moeraki Platform was highly variable. Mortality of recruits within the upper mid zone was very high and probably resulted in the low number of mature plants that were found in this area (Fig. 2.12). In contrast, recruitment in the mid zone had a similar temporal pattern to that observed in the low zone. Overall abundance of recruits did not differ between the two zones ( $F_{(1,478)} = 0.089$ ,  $p = 0.76$ ). No correlation was found between peak abundances of mature and recruit plants ( $p > 0.05$ ).

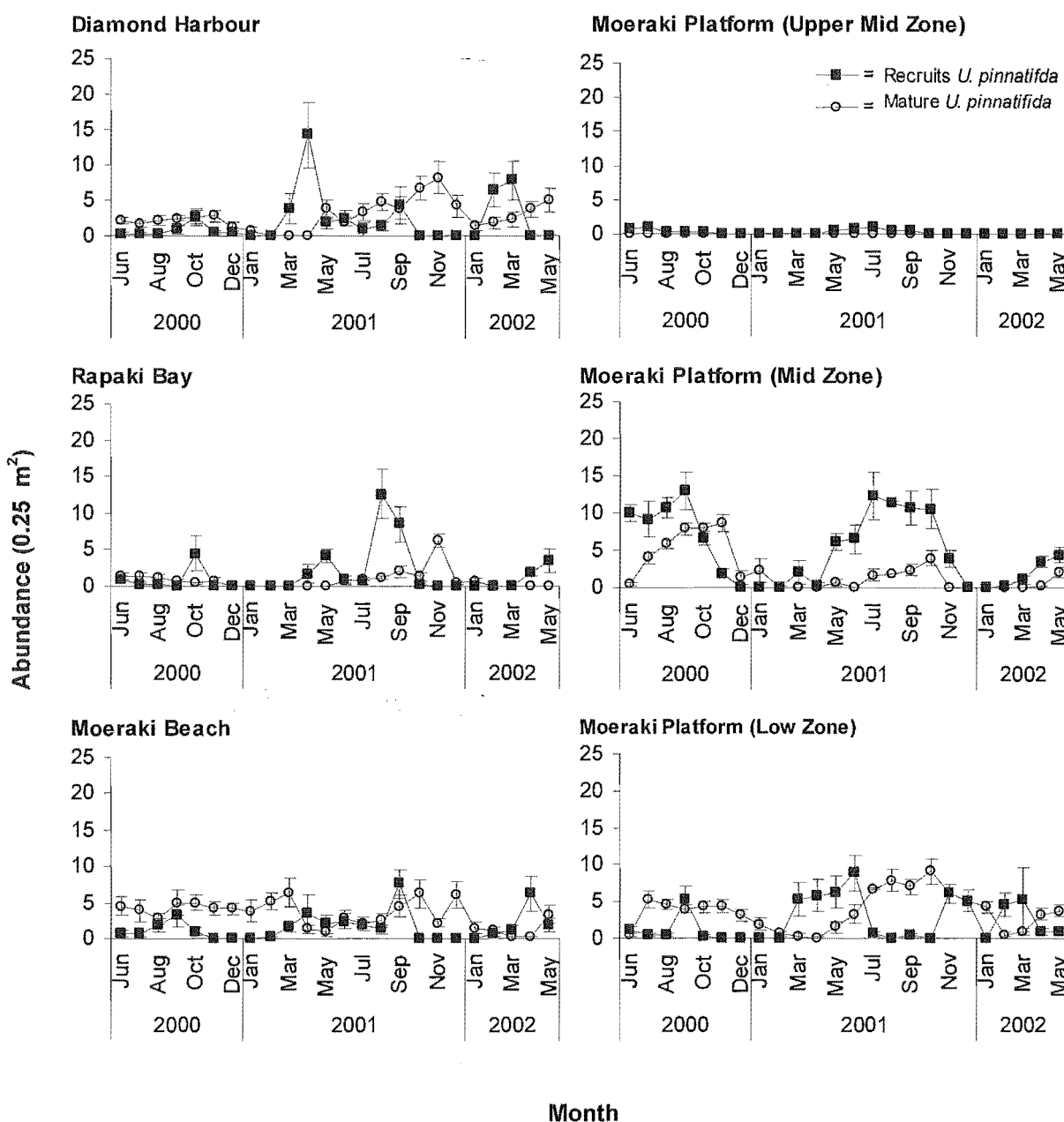


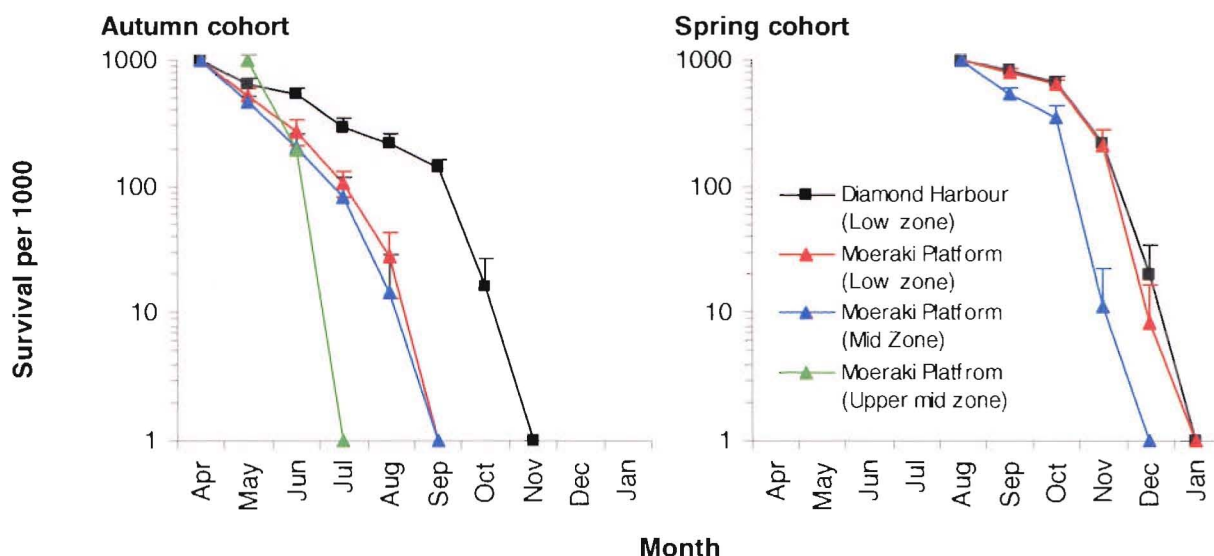
Figure 2.12: Abundance of mature and recruit *U. pinnatifida* plants between June 2000 and May 2002 ( $\pm 1$  s.e.).

### Survival

At Diamond Harbour autumn recruits survived longer than spring recruits but in the low tidal zone at Moeraki Platform there was no difference in survival times of autumn and spring cohorts (Fig. 2.13). Recruits in the mid tidal zone at Moeraki Platform survived longer during the autumn than recruits that appeared during the spring. Mortality in the upper mid zone at Moeraki Platform was very high with most plants dying by the third month. Plants did not recruit in sufficient numbers during spring to monitor survival in the upper mid zone.

Initial mortality of plants during the first three months of autumn cohorts was quite high (Fig. 2.13). During this period between 40 and 50 % of recruits were lost at each site. At Diamond Harbour, following this initial loss, recruit survival improved with only 15 % mortality observed. This increased to 40 % the following month and remained at relatively high levels between May and June. In contrast, at Moeraki Platform the low and mid zones continued to lose plants at high rates (over 40 %) throughout the same period.

Initial survival of spring cohorts at Diamond Harbour and the low tidal zone at Moeraki Platform were higher than autumn cohorts. Cohorts from both sites followed similar trajectories with the final plants disappearing after the 5<sup>th</sup> month. In comparison, survival of the spring cohort in the mid tidal zone at Moeraki Platform was much lower with plants disappearing after the 4<sup>th</sup> month. Mortality in the mid tidal zone was very high over the first two months (over 40%). This was followed by a substantial increase in mortality between October and November.



**Figure 2.13: Survival curves of mapped *U. pinnatifida* plants at Diamond Harbour, Moeraki Platform, Moeraki Platform mid zone and Moeraki Platform upper mid zone from plants that recruited in autumn and spring.  $n=10$ , (+1 S.E.).**

While plants survived longer at Diamond Harbour, they took longer to reach maturity than the plants at the Moeraki Platform (Table 2.11). Although there were site differences in maturation time there were no significant differences between seasons (Table 2.12).

Table 2.11: Average time (months) ( $\pm 1$  S.E.) taken for *U. pinnatifida* plants that recruited in autumn and spring 2001 to reach maturity. a,b,c indicate results of Tukey's HSD test; sites and season with the same letter were not significantly different at  $p < 0.05$ . Cochran's test was not significant.

Site	Autumn	Spring
Diamond Harbour	$3.64 \pm 0.12$ a	$3.66 \pm 0.14$ a
Moeraki Platform (Low zone)	$3.09 \pm 0.11$ b	$2.97 \pm 0.12$ b
Moeraki Platform (Mid zone)	$2.82 \pm 0.09$ c	$2.7 \pm 0.07$ c

Table 2.12: Results of two-way ANOVA of maturation time (in months) of *U. pinnatifida* recruits at Diamond Harbour, Moeraki Platform (low zone) and Moeraki Platform (mid zone) during autumn and spring. \*\* is significant at  $p < 0.01$ . Data were log-transformed. Cochran's test was not significant.

Effect	df	MS	F	p-value
Site	2	16.60	31.72	$p < 0.001^{**}$
Season	1	0.329	0.629	0.428
Site x Season	2	0.146	0.280	0.756
Error	240	0.523		

## 2.4 Discussion

Most studies on *Undaria pinnatifida* have focused on populations within subtidal habitats. This study is unique in that it focuses on populations that occupy the low intertidal to mid intertidal. High densities, coupled with the large size of plants, meant that much of the intertidal area at the study sites was dominated by *U. pinnatifida*. Peak densities were comparable with results from other studies done around New Zealand, but these studies were on subtidal or shallow subtidal populations (Hay and Villouta 1993; Brown and Lamare 1994). At the Moeraki Platform *U. pinnatifida* extended further into the intertidal zone than at any other site. Plants found in the mid and upper mid zones were generally smaller than plants in the low zone. Nevertheless, plants in the mid zone were still able to reach reproductive maturity.

The annual population structure of intertidal populations of *U. pinnatifida* at my sites only loosely resembles that of subtidal populations found in its native habitats of Japan, Korea and China that have peak growth and the largest plants occurring in spring- winter and the majority of senescing plants occurring over the summer-



autumn months (Saito 1975; Zhang *et al.* 1984; Koh and Shin 1990; Floc'h *et al.* 1991; Casas and Piriz 1996; Curiel *et al.* 2001). Sporophyte degeneration usually occurred during the summer months at my study sites and although this is similar to other studies from around the world (see Saito 1975; Koh and Shin 1990; Curiel *et al.* 1998) senescing plants could be found during the winter months. This suggests that intertidal populations of *U. pinnatifida* along the east coast of the South Island could reproduce during winter and possibly be responsible for the increased recruitment observed during spring. These recruits may be responsible for the persistence of populations throughout the summer at most sites. Furthermore, the year round persistence of populations coupled with the multiple recruitment episodes suggests that macroscopic *U. pinnatifida* populations are not annuals as such but aseasonal annuals with autumn cohorts possibly bi-annual. The patterns of abundance at my study sites are in contrast to the strict seasonal patterns observed in its native habitat but are similar to previous studies within New Zealand (Hay and Villouta 1993) and Brittany (Floc'h *et al.* 1991).

At Rapaki Bay the seasonal hiatus between generations is similar to what has been reported from subtidal studies of *U. pinnatifida* in Japan, Korea and China (Saito 1975; Zhang *et al.* 1984; Koh and Shin 1990). However, Rapaki Bay differs from the endemic populations in two distinct ways. First, the study population was intertidal whereas the studies on the native populations are based entirely on subtidal populations so the factors causing the breaks between generations may be different. Second, during the study, mature, immature and recruit plants were found at the same time from late autumn until early summer. This has not been recorded in its native habitat. The hiatus observed during the summer and the onset of recruitment in the autumn suggests that there is a considerable early post-settlement developmental period.

Much of the variation in annual population structure between the study populations and native populations can probably be attributed to temperature differences and the affect it has on the life history of *U. pinnatifida*. In areas with small annual ranges of temperature and maximum summer temperatures of 15- 19 °C, persistent populations of *U. pinnatifida* macrosporophytes can usually be found year round (Sanderson and Barrett 1989). In contrast, in areas with a wide annual temperature

range and summer maximum temperatures of 23- 25 °C a distinct gap occurs between generations (Sanderson and Barrett 1989). Although temperature was not measured at the study sites, the summer sea temperatures at each site rarely exceed 18 °C (Dr Janelle Reynolds-Fleming *pers. comm.*). The persistence of plants at Moeraki and Diamond Harbour throughout the year maybe attributed to the relatively low summer temperatures. However, this does not explain why plants were absent from the Rapaki Bay site. One possible explanation for the differences between Rapaki Bay and the Moeraki and Diamond Harbour sites is that at Moeraki and Diamond Harbour the intertidal areas were exposed to moderate swells and splash that continually bathed the plants in water. In contrast, plants at the more sheltered Rapaki Bay site received very little relief from desiccation by water splash. Furthermore, the plants in mid zone at Moeraki Platform showed a similar annual cycle to Rapaki Bay plants with a hiatus occurring over the summer months. Wave splash rarely extended into this zone.

The annual temperatures along the east coast of the South Island provide favourable conditions for the development of the microscopic stages of *U. pinnatifida* for most months of the year. Previous studies of *U. pinnatifida* have shown that spore release occurs between 14 °C and 23 °C (Saito 1975). In the present study, spore release was shown to occur from July until March. During July and August, sea surface temperatures are usually between 6- 8 °C (Dr Janelle Reynolds-Fleming *pers. comm.*) which is lower than the minimum 14 °C required for spore release. However, plants exposed during low tide may be subjected to higher temperatures than the surrounding water mass and may release spores prematurely. Although spore release was observed spore germination was not. The requirements for spore germination have previously been recorded at 13- 24 °C (Floc'h *et al.* 1991). One study on subtidal populations of *U. pinnatifida* in New Zealand suggested that spore germination can only occur from December to March (Stuart 1997). However, it is possible that temperatures in the intertidal may have been elevated at low tide (even with wave splash occurring) and this may have allowed spore germination to occur over longer periods. Within in the South Island of New Zealand spore release and spore germination are the only processes that could be affected by temperature. Gametophyte fertilisation has been recorded at between 5- 28 °C (Akiyama 1965, reference in Floc'h *et al.* 1991), which is well within the temperature range

experienced in the South Island. However, further studies are required to determine if germination and fertilisation are possible within the intertidal habitat during periods when sea surface temperature is sub-optimal.

Many annual laminarian algae have a life cycle that is seasonally opposite to that of *U. pinnatifida*. For example, *Postelsia palmaeformis*, *Alaria marginata*, and *Alaria nana*, which occupy wave exposed shores of the north-east Pacific, macrosporophytes appear during the early spring grow rapidly during spring and summer and reproduce during late summer (Dayton 1973; Pfister 1991, Blanchette 1996). Post-reproductive plants senesce during late autumn and by winter, all visible signs of macrosporophytes are absent. As a consequence of spring recruitment, populations of Northern Hemisphere annual species are usually absent during the winter. This contrasts to populations of *U. pinnatifida* which in its native habitat and some invaded areas are absent during the summer. The differences in life histories between *U. pinnatifida* and the aforementioned Northern Hemisphere species may mean that different mechanisms may be involved in the continual persistence of populations.

Growth of *U. pinnatifida* showed a seasonal pattern of elongation and erosion. Although growth rates were high, they were comparable with other laminarian species (Table 2.13). Other studies of the growth rates of *U. pinnatifida* in New Zealand are comparable with the results of this study. However, erosion rates observed during my study were higher. This is not surprising as the populations in this study were present in the rocky intertidal and were probably subjected to higher rates of abrasion, desiccation and whiplash. The high erosion rates meant that plant size was dictated by habitat. Plants at Diamond Harbour and the Moeraki Platform experienced higher erosion rates than the Rapaki Bay and Moeraki beach sites. This was probably due to these sites being more exposed during periods of bad weather (*per. obs.*). Although *U. pinnatifida* was subjected to high erosion rates, this did not appear to affect the overall survival of the plant as most plants that were followed through time produced a sporophyll. Growth to reproductive maturity took approximately 2-3 months from recruitment so it is conceivable that plants that recruited in April/May could reproduce by mid winter and have recruits appearing during late spring.

Table 2.13: Maximum and minimum growth rates of laminarian algae obtained from studies on seasonal growth rates. All data were collected using the hole punch method (table adapted from Stuart 1997).

Species	Growth rate (mm d <sup>-1</sup> )	Reference
<i>Alaria esculenta</i>	1-5	Buggeln 1974
<i>Ecklonia radiata</i>	7.6-19.6	Larkum 1986
<i>Costaria costata</i>	1.8	Maxell and Miller 1996
<i>L. longicruris</i>	2-10	Gerard and Mann 1979
	4-18	Gagné <i>et al.</i> 1992
	4-22	Gendron 1989
	9.2-16	Chapman and Craige 1977
<i>L. saccharina</i>	5-21	Parke 1948
	1-12	Sjøtun 1993
<i>Nereocystis luetkena</i>	32-61	Maxell and Millar 1996
<i>Pelagophycus porra</i>	22-65	Coyer and Zaugg-Haglund 1982
<i>Phyllariopsis purpurascens</i>	3-3.8	Flores-Moya <i>et al.</i> 1993
<i>Saccorhiza polyschides</i>	1-21	Norton 1969
<i>U. pinnatifida</i>	2-11.6	Stuart 1997
	0.19-14.7	Present study

Although many studies have examined the production of the number of spores per given area for laminarian very few studies have examined the potential fecundity of individual plants. Estimates of spore production per unit can vary between species. For example, *L. saccharina* can produce  $64 \times 10^6$  spores per cm<sup>2</sup> of sorus (Parke 1949). Kain (1975) reported  $3.3 \times 10^6$  spores per mm<sup>2</sup> of sorus for *L. hyperborean*. Previous estimates of spore production in *U. pinnatifida* have recorded  $1 \times 10^4$ - $1 \times 10^6$  per gram of sporophyll (Saito 1975). In comparison, estimates of total spore production for laminarians plant have produced astronomical numbers. For example, Chapman (1984b) estimated that individuals of *L. longicruris* could produce  $8.75 \times 10^9$  spores. Even larger numbers have been recorded for individuals of the giant kelp *Nereocystis leutkeana*, which estimated that  $37 \times 10^{11}$  spores are produced over the entire reproductive season (Chapman 1984b). Similar numbers of spores were recorded for individual plants of *U. pinnatifida* in this study ( $1 \times 10^9$ ). The high reproductive output of laminarians probably increases propagule pressure on the environment and may be an adaptation that has evolved in order to increase the chances of successful dispersal and recruitment within marine environments. This would suggest that the propagule pressure exerted by *U. pinnatifida* is enormous

considering the fecundity of individuals and the length of reproductive period. A possible explanation why *U. pinnatifida* is so invasive and other laminarians are not is that *U. pinnatifida* has a strong ability to attach to hulls of boats, thereby allowing greater dispersal as well as increasing propagule pressure by multiple introductions. I am unaware of any other laminarian species that can be dispersed this way.

Despite the long reproductive period and high fecundity per plant, *U. pinnatifida* recruitment of *U. pinnatifida* was highly variable through time, which is comparable with previous studies on *U. pinnatifida* in New Zealand (Hay and Villouta 1993; Stuart 1997). The results suggest that very few spores actually result in visible recruits appearing. Chapman (1984a) estimated survival rates of early post-settlement stages of *Laminaria longicruris* was approximately 0.00001 %. Similar survival rates of *U. pinnatifida* may occur but this is only speculative. Alternatively, variable *U. pinnatifida* recruitment may be due to a number of factors affecting the early post-settlement stages. Factors such as, density-dependent effects; suitable recruitment sites, desiccation, grazing, competition, spore dispersal, spore settlement, germination success and gametophyte density are all considered important determinants of recruit success (Reed 1990a; Reed *et al.* 1991; Reed *et al.* 1992; Vadas *et al.* 1992; Anderson *et al.* 1997, Reed *et al.* 1997) and may have affected recruitment success of *U. pinnatifida*.

Density-dependent effects such as self-thinning are important in the maintenance and regulation of large brown algae (Black 1974; Schiel 1985a). However, the effects of density on demography are often debated (Reed 1990b). Studies have shown that density dependent mortality can occur in even aged stands of algae (Black 1974; Schiel and Choat 1980; Chapman 1984a; Reed 1990b). However, high density can actually increase growth rates and reproductive rates (Schiel and Choat 1980& 1981; Schiel 1985a; Reed 1990b). Although density-dependent effects were not specifically tested in this study, self-thinning of *U. pinnatifida* recruits may have occurred during autumn when their abundance was greatest. In spring, lower recruitment rates were observed and this may have resulted in higher initial survival rates.

Survival curves of *U. pinnatifida* cohorts were similar to other species of laminarians such as *L. longicruris*, *Egregia laevigata* and *Macrocystis pyrifera* (Black 1974; Chapman 1984b; Dean *et al.* 1989), but initial survival of *U. pinnatifida* recruits was slightly lower (about 60%) than values recorded for other laminarian species. For example, initial survival of *L. longicruris* recruits was about 75 % (Chapman 1984b) whereas 75- 87% of *E. laevigata* recruits survived in the first month (Black 1974). The lower initial survival rates of *U. pinnatifida* may reflect density-dependent effects between new recruits. After the first month, any effects of density were possibly reduced as increased survival was observed in both autumn and spring cohorts. Similar patterns of survivorship have been observed over extended periods for *M. pyrifera* with increased survival occurring after high initial mortality (Dean *et al.* 1989). Although density-dependent effects may have occurred during the initial stages after *U. pinnatifida* recruitment properly controlled experiments would need to be done in the future to determine if this is the case.

Numerous studies have shown that shading by subtidal macroalgal canopies can inhibit recruitment of algae by reducing light levels (Dayton *et al.* 1984; Reed and Foster 1984; Dayton *et al.* 1992) Disturbance to these canopies, which provides light necessary for growth of microscopic stages (Kain 1964; Kain 1969; Chapman and Burrows 1970; Lüning 1980; Santelices 1990b; Kinlan *et al.* 2003) is usually episodic and can result in variable patterns of recruitment both spatially and temporally. In this study, populations were confined to the intertidal, which can be considered a high light environment. However, the high density of plants coupled with their large size meant that much of the substrata was completely covered. Mortality of tagged plants was extremely high at all sites so there would have been continual gaps in the canopy during most months of the year allowing recruitment. Although shading may explain some of the variability in recruitment rates, it does not explain why there was no recruitment during the summer months, a time when large gaps were formed due to most plants senescing.

The absence of recruits during the summer was surprising considering this was a period when reproductive plants were most abundant and conditions were favourable for spore germination and fertilisation. The lack of recruitment may be due to a number of factors. First, the temperatures experienced in the intertidal area

may have retarded the post-settlement development, but with the sites, being continually splashed with water it is unlikely that temperatures would have exceeded the sub optimal limits of spore germination, fertilisation and sporophyte development. This must be interpreted with some care as temperature measurements were not taken within or on the substrata in which *U. pinnatifida* recruited. Second, it is possible that during the summer months, the gametophytes underwent a period of vegetative growth, again this seems unlikely as periods of total darkness would be difficult to achieve especially as most mature plants were senescing during this time. Alternatively, it is possible that microscopic stages may be lying dormant, or growing slowly during unfavourable recruitment periods. Persistence of *P. palmaeformis* populations is thought to occur with either the spore or the gametophyte stage surviving/growing over the winter months (see Clayton 1988 for review). Alternatively, microscopic germlings of *Dictyota dichotoma* were shown to over-winter during periods of low temperatures (Richardson 1979). More recently, embryonic sporophytes of the laminarian *M. pyrifera* were shown to lay dormant for 1 month during low light and nutrient limiting conditions (Kinlan *et al.* 2003). It was suggested that the ability to delay recruitment during periods of limited resources may be a mechanism to allow the persistence of populations that are subjected to episodic disturbances (Kinlan *et al.* 2003). The initial recruitment pulse of *U. pinnatifida* observed in autumn could be due to the slow growth of microscopic sporophytes during the summer whereas the continual recruitment of plants during the winter months may be the result of gaps produced in the canopy or post-reproductive plants senescing. Recruits that appeared in either the autumn or winter cohort survived for approximately 4-5 months, but this was site dependent. The main cause of mortality was unknown but was probably the result of wave action with plants being either ripped from the substrate or abraded against the rocky substrata.

### *Dispersal*

Establishment of new populations requires the dispersal of propagules. Many kelps are thought to have limited dispersal because fertilisation of propagules can only occur once spores have settled. Consequently, spores have to settle in high enough densities for male and female gametophytes to be in close proximity for successful fertilisation to occur (Reed 1990a). Increased dispersal potential can occur if reproductive synchrony occurs. This is because greater numbers of spores are

released simultaneously, thereby allowing a greater chance that spores will settle away from the parent plant in high enough densities for fertilisation to occur. Reed *et al.* (1997) showed that reproductive synchrony in *M. pyrifera* and *Pterygophora californica* was critical for the dispersal of spores over extended distances and was likely to play a major role in recolonising areas destroyed by disturbances such as storms. The life history of annual kelps is conducive to reproductive synchrony as most populations reproduce over a discrete period. Nevertheless, very few studies have examined spore dispersal in these species.

Published studies on annual intertidal laminarian dispersal show that natural dispersal potential is poor. Dayton (1973) found that populations of *P. palmaeformis* were poor at dispersing propagules. Colonisation by recruits occurred at about 3 m from the parent plant in wave exposed areas of the north-east Pacific. Although *U. pinnatifida* shows a great deal of extended reproductive synchrony, localised dispersal from parent plants is in the scale of metres. Forrest *et al.* (2000) found that spores released in tidal currents were only effective at establishing plants 10 m down current from the source. Results from my study showed a much lower pattern of localised dispersal with the majority of spores found within 10 cm of the parent plant. However, these results must be interpreted with some caution for a number of reasons. First, the experiments were done during periods of calm weather. Stronger currents may have been able to disperse propagules further as shown in studies of spore dispersal for *M. pyrifera* (Reed *et al.* 1988). Second, the substratum used (microscope slides) was not ideal and some spores may have been dislodged. Although healthy spores tended to stick quite well in laboratory trials (*pers. obs.*), sediment observed on the slides may have dislodged spores or precluded spore settlement during the experiment. Third, although *U. pinnatifida* is the predominant laminarian at Moeraki Platform it was too difficult to determine whether all spores were those of *U. pinnatifida* or nearby populations of *M. pyrifera*. Differences in the results of my study and the Forrest *et al.* (2000) study therefore may be attributable, at least in part, to methodological differences and possibly water current differences. However, evidence from the two studies suggests that the natural dispersal of *U. pinnatifida* is limited and possibly site specific. Further studies examining variability of spore dispersal in *U. pinnatifida* at different sites are needed to confirm the localised patterns of dispersal for this species in New Zealand.



### Summary

The intertidal populations of *U. pinnatifida* along the east coast of the South Island are unique in that most other invaded areas are subtidal. The success of *U. pinnatifida* in this habitat is partly due to its demographic characteristics and the plasticity of its life history. Although *U. pinnatifida* has many characteristics that are similar to other laminarian species there are some characteristics which allow it to successfully invade. First, it has the ability to be either a strict annual or an aseasonal annual with a short macroscopic life span and is probably able to complete two generations within one year. Second, recruits are able to reach reproductive maturity in a very short time and coupled with the high reproductive potential means that the propagule pressure exerted on an area is enormous. Finally, *U. pinnatifida* has the ability to complete its life cycle under variable environmental conditions. The mechanism responsible for this probably occurs during the post settlement phase of its life cycle. The flexibility of its life cycle coupled with the demographic parameters mentioned above has meant that *U. pinnatifida* can colonise a broad range of areas and habitats outside its native environment.

## **Chapter 3**

# **Mechanisms of Establishment**

### 3.1 Introduction

The colonisation and establishment of any species is reliant on a number of biological and physical factors that interact with each other. Several intertidal studies have shown that the availability of bare space, which is usually a limiting resource, the availability of propagules and the interactions between colonising individuals and resident individuals are important in the colonisation of marine algae (Dayton 1974; Schiel 1988; Jenkins *et al.* 1999a; Airoidi 2000). The role of disturbance in promoting colonisation of species is widely recognised within the marine environment. In areas dominated by sessile species, the ability of individuals to recruit usually depends on physical disturbance such as wave action (Dudgeon *et al.* 1999), drifting logs (Dayton 1974) and boulder movement (Sousa 1979a), to create bare space, but may also depend to a large degree on biological disturbances such as grazing (Harrold and Reed 1985).

Although there is some consensus on the effects of disturbance on colonisation and establishment of species, there is debate about the importance the magnitude of disturbance has on colonisation (see Sousa 1984& 1985; Benedetti-Cecchi and Cinelli 1994; Kim and DeWreede 1996; Airoidi 1998). For example, Sousa (1985) proposed that small gaps would be colonised fastest due to smaller gaps having a greater ratio of edge to area than large gaps. This would allow small gaps to receive greater numbers of propagules per unit area than larger gaps. In contrast, Kim and DeWreede (1996) reported fastest colonisation in mid sized gaps within areas dominated by *Mazzaella cornucopiae*, *Fucus distichus* and *Pelvetiopsis limitata*. Colonisation of smaller gaps (5 x 5 cm) was much slower, reportedly due to shading and whiplash from surrounding plants (Kim and DeWreede 1996). The conflicting results observed in these types of clearance experiments suggests that the rate of colonisation of different sized areas can vary spatially and temporally and is likely to be influenced by both physical and biological variables associated with individual habitats.

In most ecosystems, the order of arrival of species after a disturbance can control which species dominate resources (Connell and Slatyer 1977). For individuals that arrive first, pre-emption of space can inhibit colonisation of new species for long periods (Berlow 1997). In marine algae, many early colonists are usually opportunistic and rely on life history characteristics and demographic characteristics to monopolise resources (Hruby and Norton 1979; Airoidi 2000). For example, in subtidal areas of the Mediterranean, differences in life history characteristics were shown to be important in competition for available space between turfing algae and various species of erect algae (Airoidi 2000). Turfing algae held an advantage over species such as *Dictyota dichotoma*, *Laurencia obtuse*, *Padina pavonica* and *Acetabularia acetabulum* (erect species) due to vegetative encroachment of cleared areas year round. Recruitment of erect species was reliant on the coincidence of disturbance and availability of bare space with reproductive season and favourable environmental conditions. In the long term, turfing species ended up preventing populations of erect species from establishing by pre-emption of space (Airoidi 2000).

Once an individual has established they may dictate further patterns of succession by inhibiting or facilitating new recruitment. For example, the presence of encrusting corallines in subtidal areas of Nova Scotia were shown to inhibit the recruitment of large fleshy algae (Johnson and Mann 1986). Previous authors suggested that the mechanism by which encrusting corallines can inhibit recruitment of other sessile organisms is by sloughing of epithallial cells from the crust surface (Masaki *et al.* 1984). This process is thought to act as an antifouling mechanism and possibly prevents invading propagules from developing fully (Masaki *et al.* 1984).

Although the inhibition of space by a species can affect the recruitment of other species within intertidal habitats, other species may have a facilitatory effect. For example, long-term survival of artificially recruited zygotes of *Pelvetia fastigiata* was increased in red algal turfs, which were thought to provide refuge from desiccation and grazing by macroinvertebrates (Brawley and Johnson 1991). Similarly, survival of the laminarian *Lessonia nigrescens* in Chile was thought to increase within turfing

corallines due to the microscopic life history stages being protected from grazing by the chiton *Enoplichiton niger* (Camus 1994).

The processes affecting the colonisation of *U. pinnatifida* within intertidal habitats along the east coast of the South Island are unknown. At Moeraki and Lyttelton there are a diverse range of coralline turfs, coupled with vast amounts of bare space within the intertidal zone. The presence of coralline turfs and the large amount of bare space suggest these components of the habitat may affect recruitment of *U. pinnatifida*. If, for example, algal turfs affect *U. pinnatifida* recruitment, this may occur through inhibition such as the pre-emption of primary space, or grazing by the mesofauna inhabiting turfs. Alternatively, algal turfs may facilitate recruitment, by reducing the amount of grazing by macrofauna, or providing relief from desiccation of microscopic stages.

This study examines the mechanisms involved in recruitment of *U. pinnatifida* within intertidal populations. The main objectives of this chapter were to test the effects of timing and size of clearances of coralline turfing algae on the establishment of *U. pinnatifida*. Sampling was also undertaken to quantify the macroinvertebrate grazing community within areas dominated by *U. pinnatifida*. This study was designed to test the following hypotheses 1) *U. pinnatifida* recruits rapidly into newly cleared areas; 2) the timing of clearance in relation to reproductive periodicity affects colonisation of newly cleared space; 3) the size and timing of clearances affect the recruitment of *U. pinnatifida*; 4) *U. pinnatifida* recruitment is influenced by the type of turfing species that are removed.

### 3.2 Methods

All experiments were undertaken in areas within the *U. pinnatifida* zone as defined in Chapter 1. In the removal experiments, the 25 x 25 cm quadrats were surveyed prior to removal to ensure that a minimum of 90% cover of turf was present. The experimental area was approximately 30 m long and 5 m for all experiments. Removal quadrats were scraped to ensure all organisms and propagules were eliminated. This also removed all crevices in the substratum. Quadrats were marked

using numbered nylon ramset bolts drilled into the substrata at each corner. Each permanent quadrat was monitored monthly using a gridded quadrat with 2.5 cm grid squares.

### **3.2.1 Effects of coralline turf on recruitment**

A removal experiment to test the effect of disturbance on the recruitment of *U. pinnatifida* was done in coralline turf habitat within the low zone of Diamond Harbour and the Moeraki Platform (see Chapter 1 for study site details). At each site quadrats were established in areas of similar tidal height and wave action. Three replicate, permanent 25 x 25 cm treatment and control quadrats were randomly placed at monthly intervals from November 2000 until June 2001. Treatments involved the removal of coralline turf as described above. Each quadrat was monitored for recruitment of *U. pinnatifida* for one year from initiation of the clearance. The periods chosen coincided with peak reproductive output (November- January) and periods of low reproductive output (March- May). Recruits were defined as plants <50 mm in total length. As a note, "new plants" are readily distinguished from older plants that have been damaged and are <50 mm in length. The experiment was designed to be analysed using a multi-factorial repeated measures ANOVA. However, due to some treatments having all zeros, ANOVA could not be done. Instead, cumulative abundance of new recruits were analysed using ANOVA. Prior to analysis, data were tested for homogeneity of variances using Cochran's test.

### **3.2.2 Effects of size of clearance of coralline turf on recruitment**

A removal experiment examining the ability of *U. pinnatifida* to recruit into disturbances of different sizes (i.e., areas) was done at Diamond Harbour. Four clearances of each of 5 x 5 cm, 10 x 10 cm and 25 x 25 cm, were initiated during November 2000 and October 2001. Quadrats greater than 25 x 25 cm were not used due to patches of coralline turf rarely exceeding these dimensions. Clearances and controls were monitored for recruits until May 2001 and May 2002 respectively. The experiment was designed to be analysed using a multi-factorial repeated measures ANOVA. However, due to some treatments having all zeros, this ANOVA could not

be done. Instead, two-way ANOVAs were done on the cumulative number of recruits with time and substratum used as independent factors (both fixed factors). Prior to analysis, data were tested for homogeneity of variances using Cochran's test.

### **3.2.3 Effects of turf species on *Undaria pinnatifida* recruitment.**

Discrete areas of the small brown turfing species *Halopteris congesta* were found amongst *U. pinnatifida* and coralline turf at Diamond Harbour. To test the effects of disturbance on the recruitment of *U. pinnatifida* within different turf species a removal experiment was done within the low tidal zone at Diamond Harbour. Three replicate 25 x 25 cm treatment and control quadrats were placed during November 2000 and October 2001. Treatments included different quadrats cleared of coralline turf and *H. congesta*. Controls were fixed quadrats placed within undisturbed areas of each turf species. Prior to removal, each quadrat was monitored for all species present. After the initiation of clearances, each quadrat was monitored for 7 months for recruitment rates of both species.

### **3.2.4 Natural recruitment of *Undaria pinnatifida* onto different substrata**

During autumn of 2001 and 2002, the natural recruitment of *U. pinnatifida* onto different substratum was measured within the low tide zones at Diamond Harbour and the Moeraki Platform. Substrata were grouped into six different categories that included coralline turf, encrusting corallines, cracks and crevices, bare rock, other turfing algae and 'other' (empty mussel and oyster shells, bryozoan spp. and flotsam). Five 25 x 25 cm quadrats were randomly placed within each of substrata groups. Natural recruitment data were analysed using two-way ANOVA with site and substrata as independent factors (both fixed factors). Prior to analysis, data were tested for homogeneity of variances using Cochran's test. Data were log-transformed to achieve normality.

### 3.2.5 Substratum cover and grazer abundance

Quarterly sampling was done between April 2000 and October 2002 at both Lyttelton Harbour sites and Moeraki Platform to get an estimate of percentage cover of bare space and coralline turfs and abundance of grazing invertebrates present within areas occupied by *U. pinnatifida*. Ten 1 m<sup>2</sup> gridded quadrats (with 10 x 10 cm grids) were randomly placed within the experimental areas, and percentage cover and number of species were quantified. I was not interested in seasonal variability of either percent cover or number of invertebrate grazers so temporal results were pooled for analysis. Percentage cover of bare space and coralline turfs were converted into ratios (coralline turf: bare space) and differences between sites examined using one-way ANOVA. Differences in *Turbo smaragdus* abundance between sites was analysed using one-way ANOVA. Prior to analysis, data were tested for homogeneity of variances using Cochran's test. Appropriate transformations were done as required to achieve normality. Multiple comparisons of means were done using post-hoc tests (Tukey's HSD test) and were performed on significant results ( $p < 0.05$ ) to determine differences between treatments.

## 3.3 Results

### 3.3.1 Effects of coralline turf on recruitment

The coralline turf had a significant positive effect on *U. pinnatifida* recruitment at both sites during all months the experiment was done (Fig. 3.1, Table 3.1) (data from Moeraki Platform were excluded from the analysis due to clearance treatments in most months the experiment was initiated having no recruits after 12 months). Although most recruits occurred in the coralline turfs at both sites, greater cumulative numbers of new recruits occurred at Moeraki Platform ( $14.79 \pm 1.55$ ) in comparison to Diamond Harbour ( $10.45 \pm 1.55$ ) (Table 3.2). The month in which the experiment was initiated had no effect on cumulative recruit abundance (Table 3.2).



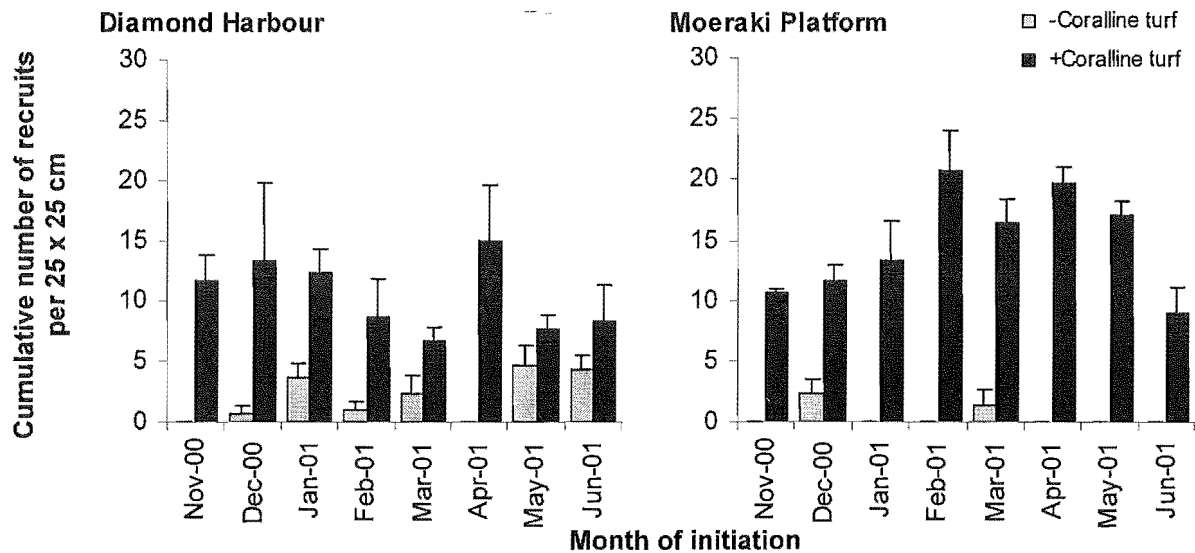


Figure 3.1: Mean cumulative number of new *U. pinnatifida* recruits (+1 S.E.) found in cleared and uncleared areas of coralline turf after 12 months for experiments initiated at different times. The x axis represents the month treatments were initiated. The y axis represents the total number of new recruits found over 12 months from the date of initiation.

Table 3.1. Results of two-way ANOVA performed on the cumulative number of new *U. pinnatifida* recruits at Diamond Harbour. (Month = December 2001, January, February, March, May and June 2002) November 2001 and April 2002 removed from analysis due absence of plants in cleared treatments, (treatment = +coralline turf, -coralline turf). Cochran's test was not significant.

Effect	df	MS	F	p- level
Month	5	10.361	0.548	0.737
Treatment	1	406.694	21.531	p<0.01
Month x Treatment	5	20.094	1.063	0.404
Error	24	18.889		

Table 3.2. Results of two-way ANOVA performed on the cumulative number of new *U. pinnatifida* recruits within +coralline turf treatments at Diamond Harbour and Moeraki Platform. (Site = Diamond Harbour and Moeraki Platform), (Month = November 2001- June 2002). Cochran's test was not significant.

Effect	df	MS	F	p- level
Site	1	225.333	9.479	p<0.01
Month	7	39.036	1.642	0.159
Site x Month	7	43.143	1.815	0.118
Error	32	23.771		

Initiation of clearances between November and December, a time when plants were at peak reproduction, resulted in no plants recruiting during the following autumn (March – May) (Fig. 3.2). In contrast, the uncleared areas had small but variable amounts of recruitment over the autumn months. During the summer months, ephemeral algae such as *Stictosiphonia* spp. and *Ectocarpus* spp. recruited into some of the newly cleared treatments at both sites, and in some instances, covered quite large areas (Fig. 3.3, Fig. 3.4). Encrusting coralline algae were found growing in many of the bare areas after a period of time (Fig. 3.3, 3.4). Greater amounts of encrusting corallines were found at Moeraki Platform (Fig. 3.4) than at Diamond Harbour (Fig. 3.5).

Further recruitment occurred during spring at both sites. Although the majority of recruitment occurred in the control quadrats, some recruits were found in the cleared areas at both sites after almost one year. Closer inspection showed that these individuals had recruited into small patches of coralline turf that had re-established or had encroached in from the edges of quadrat.

The grazing gastropod *Turbo smaragdus* was found almost exclusively within cleared treatments (Fig. 3.5). Some snails were found within turf treatments but their abundance was very low. Most snails observed within quadrats of both treatments had closed operculums so it was highly unlikely that they were feeding.

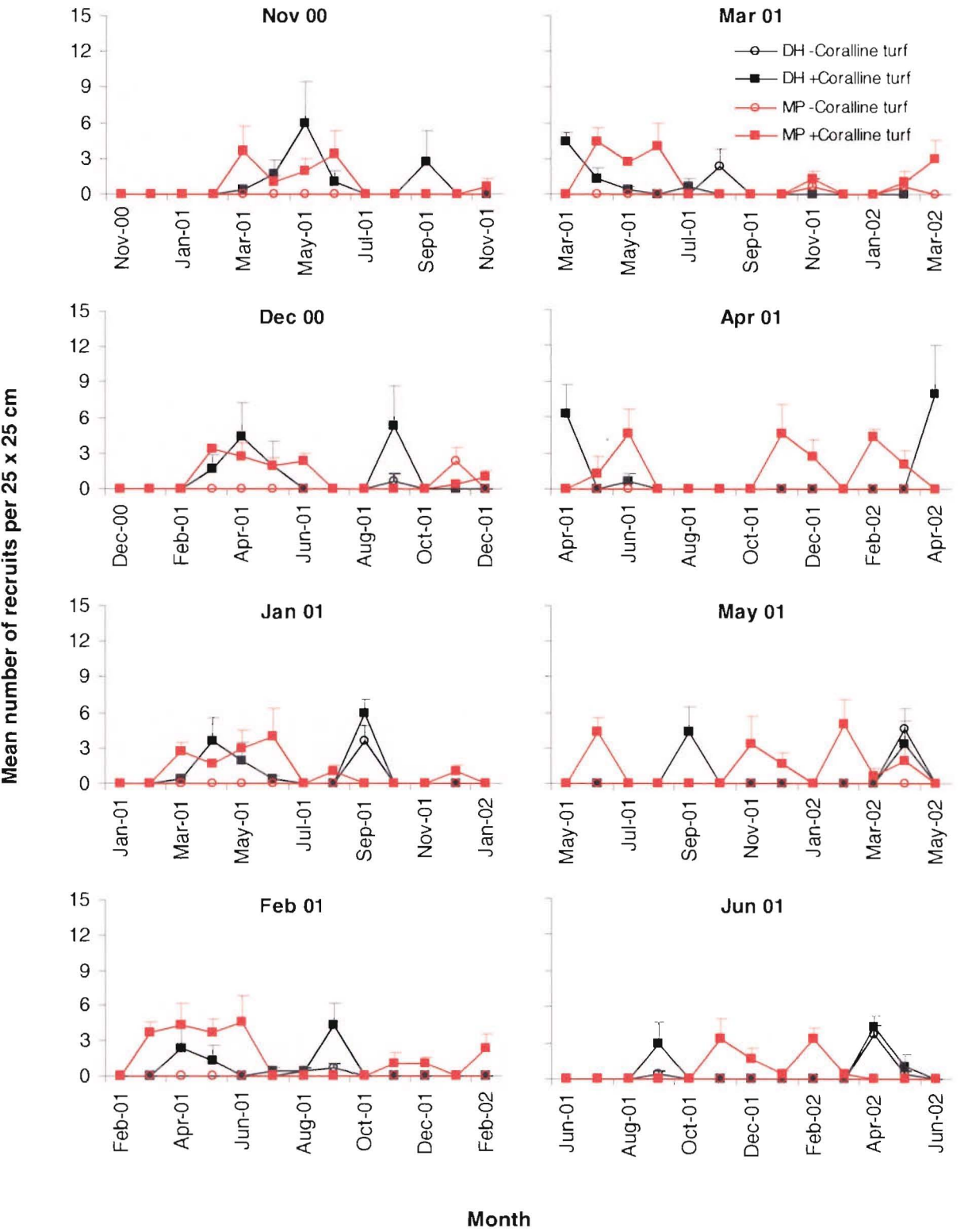


Figure 3.2: Mean number of new *U. pinnatifida* recruits per 25 x 25 cm (+1 S.E.) in uncleared areas and cleared areas of coralline turf at Diamond Harbour (DH) and Moeraki Platform (MP). Each graph represents the month in which the experiment was initiated. Sampling was done every month for 12 months (x axis).

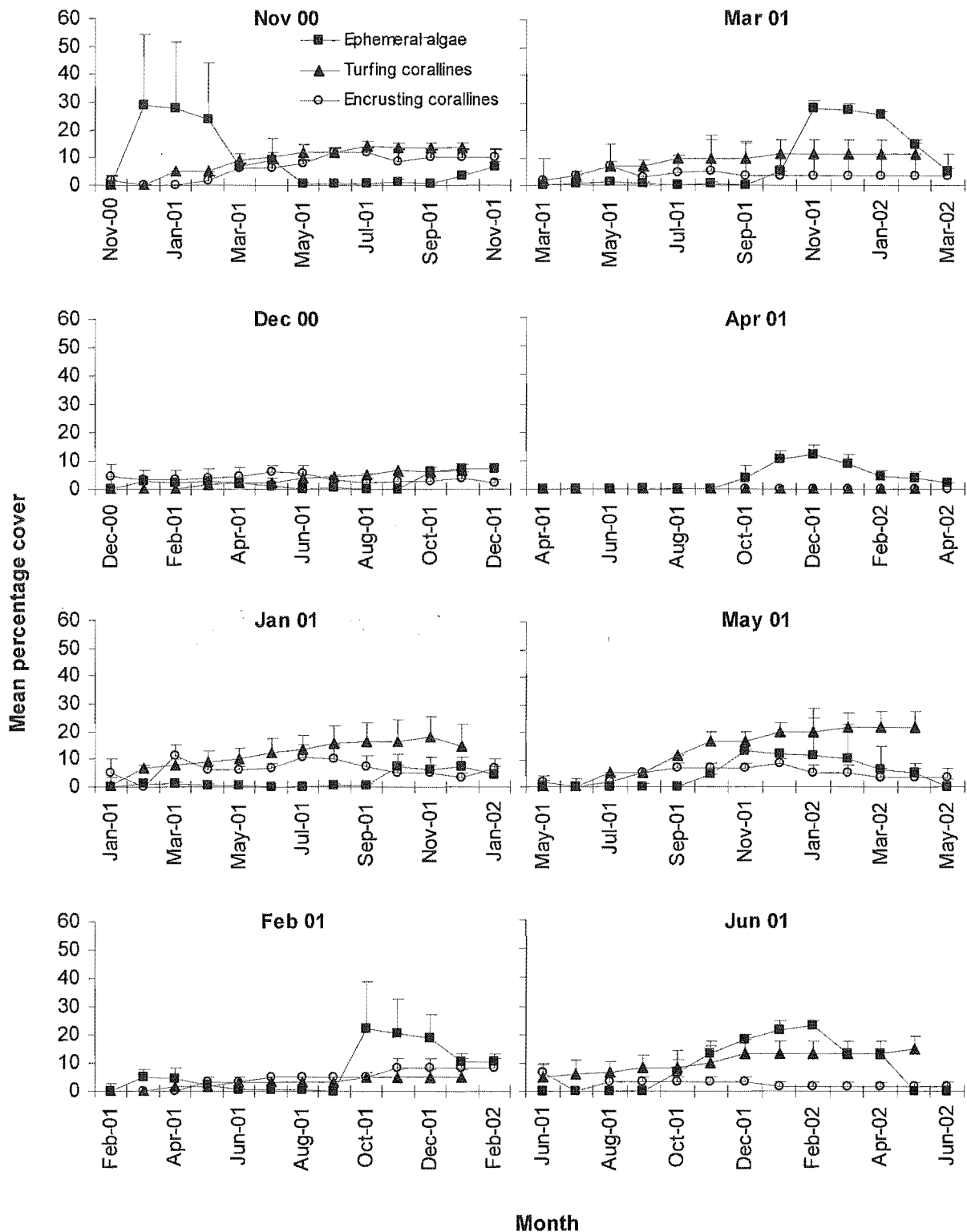


Figure 3.3: Mean percent cover (+1 s.e.) of ephemeral algae, coralline turf and encrusting corallines per 25 x 25 cm within cleared areas of coralline turf at Diamond Harbour. Each graph represents the month in which the experiment was initiated. Sampling was done every month for 12 months (x axis).

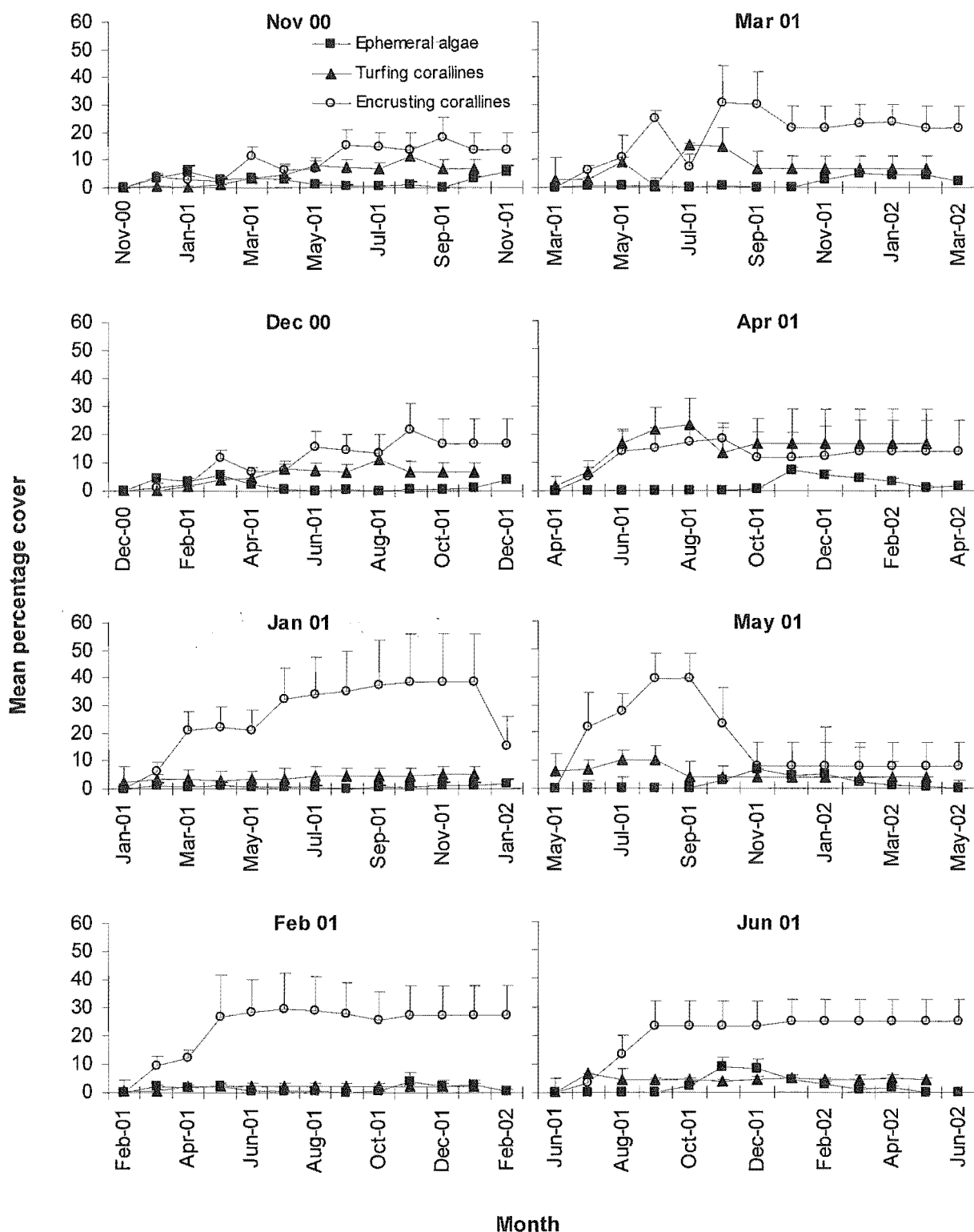


Figure 3.4: Mean percent cover (+1 S.E.) of ephemeral algae, coralline turf and encrusting corallines per 25 x 25 cm within cleared areas of coralline turf at Moeraki Platform. Each graph represents the month in which the experiment was initiated. Sampling was done every month for 12 months (x axis).

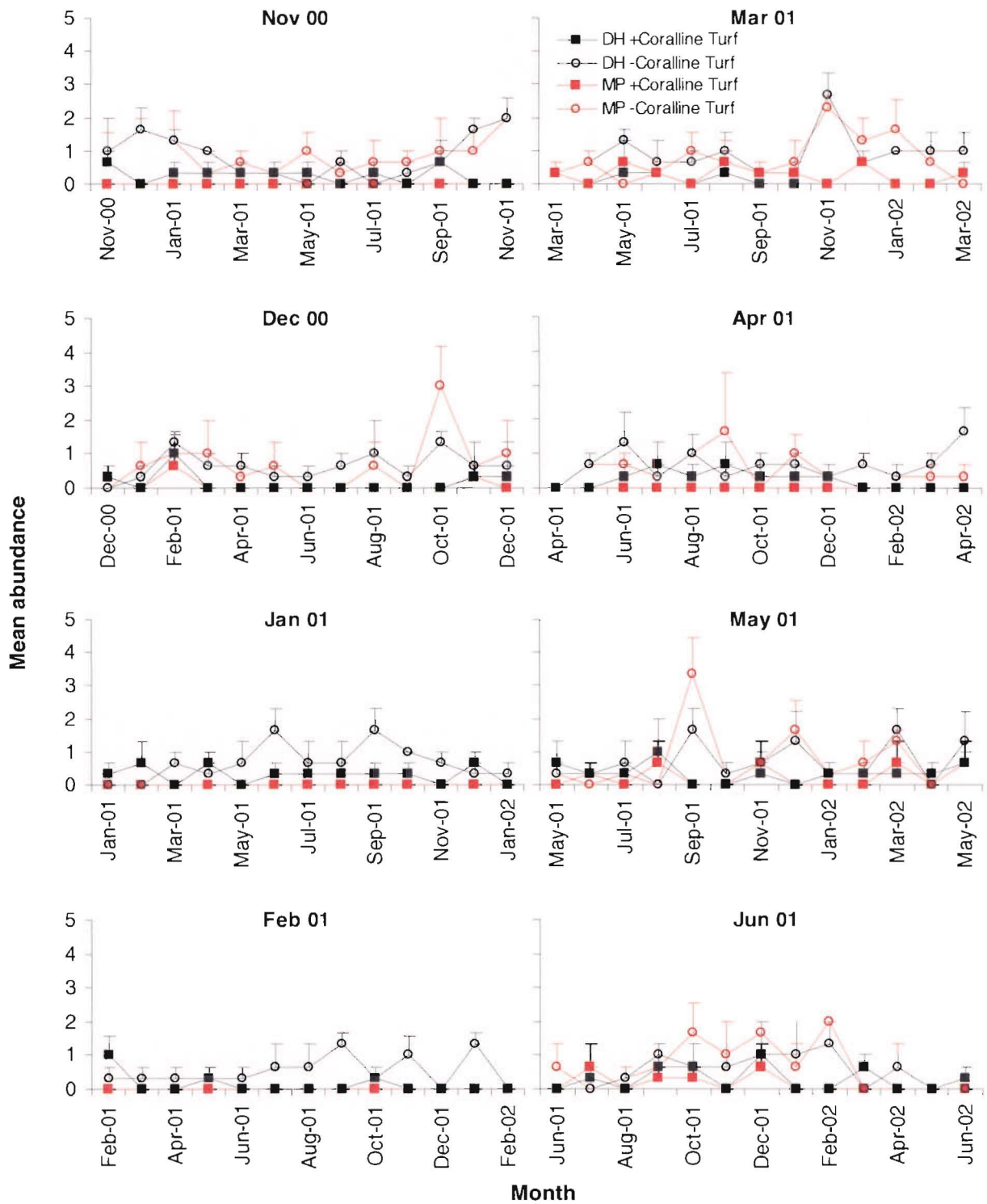


Figure 3.5: Mean abundance per m<sup>2</sup> (+1 S.E.) of *T. smaragdus* per 25 x 25 cm within cleared and uncleared areas of coralline turf at Diamond Harbour and Moeraki Platform. Each graph represents the month in which the experiment was initiated. Sampling was done every month for 12 months (x axis).

### 3.3.2 Effects of size of clearance of coralline turf on recruitment

The majority of *U. pinnatifida* recruits were found among the control areas during the autumn following the initiation of both experiments (Fig. 3.6). Size of clearance or the year in which it was done had no effect on recruitment of *U. pinnatifida* (Fig. 3.6, Table 3.3). Over the entire experiment, however, the cumulative abundance of recruits differed significantly between the cleared and uncleared treatments for the 25 x 25 cm clearances (Fig. 3.6, Table 3.4). For both experiments, observations indicated that the few recruits found in cleared areas were associated with re-established coralline turf.

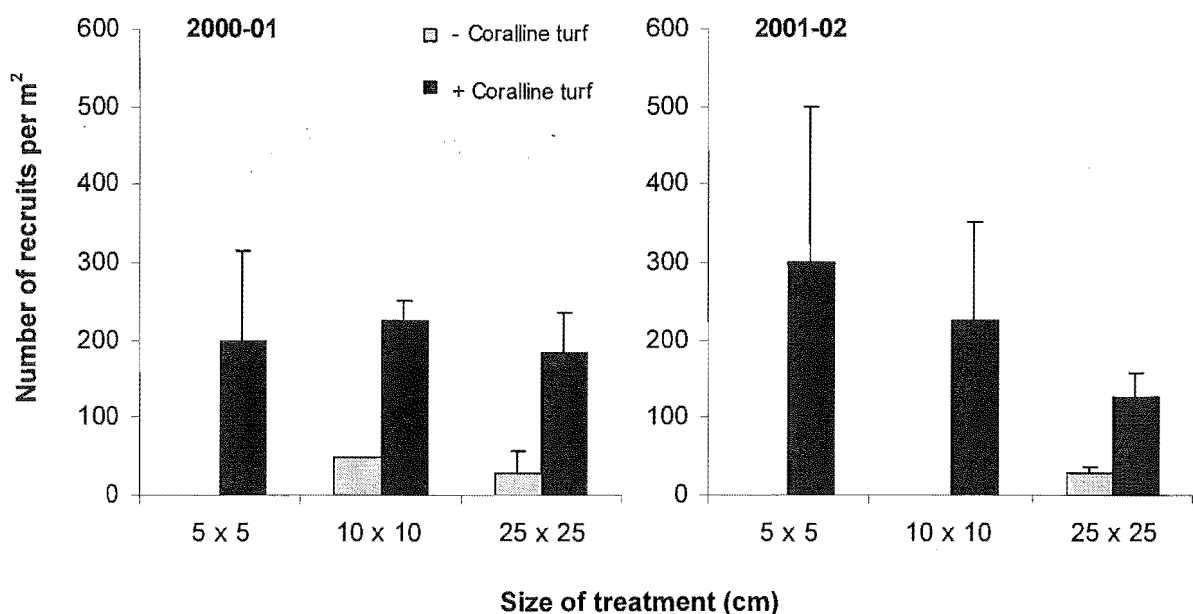


Figure 3.6: The mean abundance of *U. pinnatifida* recruits (+1 S.E.) within different sizes of cleared and uncleared areas of coralline turf. The 2000-01 experiment was initiated during November 2000 and recruits were recorded between March 2001 and May 2001. The 2001-02 experiment was initiated during October 2001 and recruits were recorded between February 2002 and April 2002. Recruit abundance is standardised to 1 m<sup>2</sup>.

Table 3.3: Results of two-way ANOVA performed on the cumulative number of *U. pinnatifida* plants recruiting (standardised to 1 m<sup>2</sup>) in different sized +turf treatments during autumn 2001 and 2002 at Diamond Harbour. Data were log-transformed. Cochran's test was significant.

Effect	df	MS	F	p- level
Year	1	0.857	0.237	0.63
Size	2	5.645	1.562	0.23
Year x Size	2	1.896	0.525	0.60
Error	18	3.613		

Table 3.4: Results of two-way ANOVA performed on the cumulative number of *U. pinnatifida* plants recruiting (standardised to 1 m<sup>2</sup>) in 25 x 25 cm + coralline turf and -coralline turf treatments during autumn 2001 and 2002 at Diamond Harbour. Data were log-transformed. Cochran's test was not significant.

Effect	df	MS	F	p- level
Year	1	0.039	0.208	0.656
Treatment	1	11.220	60.279	p<0.01
Year x Treatment	1	0.110	0.588	0.458
Error	12	0.186		

### 3.3.3 Effects of turf species on *Undaria pinnatifida* recruitment.

There was a considerable turf species effect on the recruitment rate of *U. pinnatifida* in both years the experiments were done. All but one of the recruits observed were found within the coralline turf (Table 3.5).

Table 3.5: Cumulative number of *U. pinnatifida* recruits over seven months found in each treatment at Diamond Harbour.

	Initiated November 2000	Initiated October 2001
Treatment	# of recruits per 625 cm <sup>2</sup>	# of recruits per 625 cm <sup>2</sup>
+ Coralline turf	24	14
- Coralline turf	0	0
+ <i>Halopteris congesta</i>	0	1
- <i>Halopteris congesta</i>	0	0



### 3.3.4 Natural recruitment of *Undaria pinnatifida* onto different substrata

The majority of recruits were found within patches of turfing coralline at both sites (time was not significant ( $p < 0.01$ ) so data were pooled within site) (Table 3.6, 3.7). The high numbers of recruits found on coralline turf resulted in significant differences between the sampled substrata (Table 3.6). At the Moeraki Platform, small numbers of recruits were found within the eroded holes of the burrowing bivalve *Pholid* sp. (Table 3.7, cracks/crevices). At Diamond Harbour some recruits were found within small crevices and on prostrate pieces of *H. congesta*. At both sites recruits were also found in small numbers on a variety of other substrata that included mussel beds and empty oyster shells. One recruit was found on a bryozoan colony at Diamond Harbour while two recruits were found on pieces of flotsam that were wedged into the rocks at the Moeraki Platform.

**Table 3.6: Results of two-way ANOVA performed on occurrence of natural recruitment of *U. pinnatifida* on coralline turf, cracks and crevices, turf species and other substrata at Diamond Harbour and the Moeraki Platform during autumn 2001 and 2002. Data were log-transformed. Cochran's test was not significant.**

Effect	df	MS	F	p-value
Site	1	0.023	0.190	0.664
Substratum	3	13.816	109.773	$p < 0.01$
Site x Substratum	3	0.063	0.499	0.684
Error	72	0.126		

**Table 3.7: Mean number of *U. pinnatifida* recruits  $\pm 1$  s.e. on different substratum at Diamond Harbour and Moeraki Platform during autumn 2001 and 2002. a,b indicate results of Tukey's HSD test; sites with the same letter were not significantly different at  $p < 0.05$ .**

Substratum	Diamond Harbour	Moeraki Platform
Coralline turf	$6.2 \pm 0.78$ a	$5.7 \pm 0.89$ a
Encrusting coralline	0	0
Bare	0	0
Cracks/crevices	$0.6 \pm 0.22$ b	$0.9 \pm 0.27$ b
Other turf species	$0.1 \pm 0.1$ b	$0.2 \pm 0.13$ b
Other	$0.2 \pm 0.13$ b	$0.2 \pm 0.13$ b

### 3.3.5 Substratum cover and grazer abundance

There were significant differences in the ratio of coralline turf: bare space at each of the sites ( $F_{(2,236)} = 100.73$ ,  $p < 0.01$ ). Diamond Harbour had a greater ratio of coralline turf: bare space ( $6.9 \pm 0.75$ ) than either Rapaki Bay ( $0.82 \pm 0.08$ ) or Moeraki Platform ( $2.48 \pm 0.30$ ). At Rapaki Bay similar percentage cover of coralline turf and bare space were found.

The turbinid snail *Turbo smaragdus* was significantly more abundant at Moeraki Platform than at any of the other sites ( $F_{(2,357)} = 649.95$ ;  $p < 0.01$ ) (Table 3.8). The small *Cantharidus* sp. snails were abundant at Moeraki Platform, but were not found at Lyttelton. *Haliotis iris* were found at Lyttelton Harbour sites in small numbers ( $< 1\text{m}^2$ ). The most notable differences observed between the sites were the absence of a number species at the Moeraki Platform including *Cellana* spp., *Melagraphia aethiops*, *Chiton pelliserpentis* and *Patelloidea* spp. *Cookia sulcata* was encountered in very small numbers ( $< 0.1\text{m}^2$ ) at Moeraki Platform but not at the other sites.

Table 3.8: Mean number per  $\text{m}^2$  of grazing invertebrates  $\pm 1$  S.E. at Diamond Harbour, Rapaki Bay and Moeraki Platform between April 2000 and October 2002. One-way ANOVAs were performed on *Turbo smaragdus* abundance with site as the independent factor. Data were log-transformed. Cochran's test was not significant. a,b,c indicate results of Tukey's HSD test; sites with the same letter were not significantly different at  $p < 0.05$ .

Species	Diamond Harbour	Rapaki Bay	Moeraki Platform
<i>Cellana</i> spp	$1 \pm 0.23$	$0.11 \pm 0.05$	0
<i>Chiton pelliserpentis</i>	$0.3 \pm 0.10$	$0.20 \pm 0.05$	0
<i>Melagraphia aethiops</i>	$0.3 \pm 0.08$	$1.12 \pm 0.34$	0
<i>Patelloidea</i> spp	$0.2 \pm 0.06$	$1.23 \pm 0.04$	0
<i>Haliotis iris</i>	$0.1 \pm 0.04$	$0.15 \pm 0.11$	0
<i>Turbo smaragdus</i>	$3.86 \pm 0.47$ a	$7.7 \pm 0.59$ b	$53.63 \pm 1.9$ c
<i>Cantharidus</i> spp	0	0	$5.4 \pm 0.9$

### 3.4 Discussion

This study clearly showed that primary bare space was not a requirement for the recruitment of *U. pinnatifida* and that by far the most recruitment occurred within

patches of coralline turf. The provision of bare space, regardless of size and timing, resulted in areas being colonised by invertebrates and other algal species, but not by *U. pinnatifida*. Instead, it appears that the turfing corallines facilitate the recruitment of *U. pinnatifida* within the intertidal zone. The facilitation of recruitment appeared to be species-specific with more recruits appearing amongst coralline turfs than on the brown turf *Halopteris congesta*.

Although both facilitation and inhibition of turfing algae on recruitment have been demonstrated in many studies, inhibitory effects of turfing algae are more common (Vadas *et al.* 1992). In subtidal studies, the recruitment of the large brown kelp *Macrocystis pyrifera* was inhibited by the presence of canopies and turfs (Dayton *et al.* 1984). Schiel (1985b) found that the presence of *Calliarthron tuberculosum* had a strong negative affect on recruitment of *Cystoseria osmundacea*. Harris *et al.* (1984) found that coralline turfs affected the recruitment of kelps both directly and indirectly after storms. Herbivorous fish could feed on recruits that had settled within the regenerating turfs, whereas recruits that settled within the tall filamentous brown algae had greater survival (Harris *et al.* 1984). Many intertidal studies have shown the dramatic negative effects of turfs on the recruitment of macroalgal species, but very few have suggested the mechanisms behind the lack of recruitment (Hruby and Norton 1979; Sousa 1979a; Sousa *et al.* 1981; Foster 1982). Vadas *et al.* (1992) alluded to grazing, chemical antibiosis and sedimentation as possible mechanisms for the lack of recruits in such studies.

Facilitation, of recruitment by turfing algae can occur by a range of mechanisms (Brawley and Johnson 1991; Benedetti-Cecchi and Cinelli 1992; Brawley and Johnson 1993; Camus 1994; Schiel and Taylor 1999). Brawley and Johnson (1993) suggested that increased survival of the fucalean *Pelvetia compressa* was due to turfing corallines trapping sediments and preventing scouring of recruits. Recruitment of the fucoid alga *Hormosira banksii* in New Zealand depends on substratum type (Schiel and Taylor 1999). At sites with a hard reef, *H. banksii* recruited directly onto bare rock, but at other sites where the substratum was less stable, successful recruitment was facilitated by the presence of both encrusting and short-turfing coralline algae.

Coralline turfs may also provide a refuge for recruits of *U. pinnatifida* from macroinvertebrate grazers. Camus (1994) observed higher numbers of recruits of *Lessonia nigrescens* within the turfing alga *Corallina officinalis*. It was suggested that the *C. officinalis* facilitated the recruitment of *L. nigrescens* due to the inability of the chiton *Enoplichiton niger* to graze effectively amongst the turf. Other studies have also shown the ineffectiveness of macroinvertebrate grazers to graze turfs. (Underwood and Jernakoff 1981; Jernakoff 1985). The structural complexity of densely branched coralline turfs is thought to result in lower gastropod abundance and reduced grazing pressure (Kelaher 2002, 2003a&b). In my study, very few grazers were found within the coralline turf treatments. The turfing species at my sites were generally short (<2 cm), densely packed and may have prevented large grazers from removing propagules. However, further studies would be needed to determine if coralline turf structure could inhibit grazing.

Another likely explanation for increased recruitment within coralline turfs is that they provided shelter for recruits from extreme environmental conditions. Desiccation, light and temperature may all have been more intense on open surfaces (Davison and Pearson 1996) and algal propagules are known to be particularly susceptible to these stresses (Schonbeck and Norton 1978; Lüning 1980; Brawley and Johnson 1991; Vadas *et al.* 1992; tom Dieck 1993). For example, survival of early post-settlement stages of *P. fastigata* is greatly reduced on bare substrata exposed at low tide. When propagules settle within moist microhabitats survival is greatly increased (Brawley and Johnson 1991). In my study, most *U. pinnatifida* recruits were found within areas, which were kept relatively moist during exposure at low tide (such as cracks, crevices and turf). Gibbons (1988) found that accumulation of sediments within low shore "artificial coralline turfs" resulted in water retention within the mats. Water retention by turfing corallines may be the mechanism that allows *U. pinnatifida* to recruit within the intertidal at Moeraki Platform and Diamond Harbour. My study areas were subjected to frequent periodic sedimentation during bad weather, and subsequent inspection showed accumulation of sediments within the turfs. Although *U. pinnatifida* recruitment may be facilitated by coralline algae further studies are required to determine the mechanism(s) and processes involved before any conclusions can be drawn.

Although facilitation of recruitment may occur, there are several other possible explanations for the lack of recruits within the newly-cleared areas. One is that *U. pinnatifida* may have been out-competed by ephemeral algae. Ephemeral algae such as *Stictosiphonia* spp. and *Ectocarpus* spp. recruited rapidly into most quadrats cleared during the summer. The newly-recruited ephemeral algae may have smothered *U. pinnatifida* spores or gametophytes so that ambient light intensity may have fallen below the critical levels required for gametogenesis. Alternatively, high light on bare surfaces may have killed all *U. pinnatifida* gametophytes. In species of *Laminaria*, gametophytes could not survive for more than 30 min when exposed to direct sunlight (Lüning 1980).

It is equally possible that grazing may have resulted in the absence of recruits in newly-cleared areas. At Moeraki Platform, high numbers of the grazing gastropod *Turbo smaragdus* were found within areas occupied by *U. pinnatifida*. Furthermore, more *T. smaragdus* were found within cleared experimental plots than in the control plots at both sites. Although grazing was not observed directly in this study, previous studies have shown that gastropod grazers can have a substantial negative effect on recruitment of macroalgae. Walker (1998) found that high densities of *T. smaragdus* (5 and 10 per 33 x 33 cm) had a significant negative impact on developing assemblages of coralline turfs and ephemeral species at Moeraki and Kaikoura. It is therefore possible that grazing may have had an effect on *U. pinnatifida* recruitment within primary bare space at both study sites. Consequently, hypotheses about the effect of grazing on survival of early post-settlement stages of *U. pinnatifida* are tested in the following chapter (Chapter 5).

Finally, lack of recruits within the bare quadrats at both Diamond Harbour and the Moeraki Platform may be the result of site-specific processes. At Moeraki, the platform is predominantly mudstone with a fine layer of sediment over most bare areas. This may affect the ability of spores or gametophytes to adhere to the surface (Airoidi 2003). In contrast, the substratum at Diamond Harbour is basaltic and very stable but re-suspension of silt particles from the seafloor can occur during bad weather. Although sediments can affect settlement of propagules, settled propagules may suffer severe stress and mortality by smothering from sediments (Airoidi 2003).

For example, in laboratory experiments sediment prevented the attachment of *Macrocystis pyrifera* spores and development of gametophytes (De Vinny and Volse 1978). In *U. pinnatifida*, sediments were shown to inhibit germ tube insertion, spore germination and maturation of gametophytes (Arakawa and Matsuike 1992 cited in Airolidi 2003). Although sedimentation effects were not examined in this study, it is possible that interactions between coralline turfs and sediments may play an important role in recruitment of *U. pinnatifida*. Future studies examining the effect of sedimentation on recruitment would be beneficial and may provide insight into habitat use by this species within the intertidal zone.

### *Summary*

Connell and Slatyer's (1977) facilitation model states that "the entry and growth of the later species is dependent upon the earlier species "preparing the ground"; only after this can the species colonise. The evidence from this study suggests that the presence of coralline turf is a major determinant in the recruitment success of *U. pinnatifida* within intertidal areas. Future expansion of *U. pinnatifida* within intertidal areas may require the presence of facilitatory species "to prepare the ground" for this species to establish. The mechanism(s) of facilitation are unclear at this stage but further studies examining grazing and desiccation may provide some useful insight.

## **Chapter 4**

# **Canopy Disturbance**

## 4.1 Introduction

An important factor in the structuring of many terrestrial and marine communities is the availability of gaps within canopies (Connell *et al.* 1997). In marine systems, canopy gaps allow opportunities for understory species and propagules of canopy-forming species to establish by providing light and space necessary to grow and establish (Foster 1975; Pearse and Hines 1979; Reed and Foster 1984; Connell *et al.* 1997). The initiation of gaps is often episodic and is usually associated with storms (Reed *et al.* 1988), grazing (Pearse and Hines 1979) or wave action (Paine 1979). In numerous studies, canopy removal experiments mimicing natural clearances by storms or grazing (Kennelly 1987a, 1987b) have shown the importance of canopy disturbance for recruitment (Reed and Foster 1984; Santelices and Ojeda 1984; Schiel and Foster 1986; Graham *et al.* 1997). For example, Reed and Foster (1984) found that the canopy of *Macrocystis pyrifera* and *Pterygophora californica* reduced the amount of light reaching the substratum by 97-99%. Experimental removal of both canopies resulted in increased levels of recruitment of *M. pyrifera*, *P. californica* and *Desmarestia ligulata*, and was most likely caused by increased irradiance reaching the substratum.

The timing of formation of canopy gaps relative to the reproductive periods of different algae can be a major factor in determining which species are available to occupy new space (Dayton 1975; Schiel 1988; Reed *et al.* 2000). Generally, the appearance of gaps is episodic, so the ability of a species to recruit depends largely on when gaps appear relative to reproductive activity. In northern New Zealand, removal of the *C. maschalocarpum* canopy during its reproductive period (November- February) resulted in recruitment dominated by fucalean species including *Carpophyllum* spp. and *Sargassum sinclairii*, and only small numbers of the laminarian *Ecklonia radiata*. Over time, *C. maschalocarpum* regenerated to form dense canopies (Schiel 1988). When removals were done during winter (outside its reproductive period) small numbers of *E. radiata* recruited over the first three months and small numbers of fucalean species recruited during the summer, but the *C. maschalocarpum* clearances did not recover to their former abundances (Schiel 1988). The differing patterns of recruitment were largely explained by the timing of



disturbance in relation to reproductive periodicity and the dispersal capabilities of each species (Schiel 1988).

The relationship between timing of canopy disturbance and reproduction can be altered if there are "seed banks" or microscopic stages that can persist and then take advantage of light gaps when they appear. For example, at least some algal species may have delayed recruitment in low light conditions (Kain 1964; Novaczek 1984b; Bolton and Levitt 1985; Edwards 1998 & 2000; Kinlan *et al.* 2003). Delayed recruitment may be caused by the ability to suspend development of either the gametophytes or embryonic sporophytes during low light periods (Kain 1964; Richardson 1979; Kinlan *et al.* 2003). If this occurs in the field, then propagules lying beneath the canopies would appear irrespective of reproductive seasonality (Kimura and Foster 1984).

Delayed recruitment may be a possible mechanism that *Undaria pinnatifida* uses to invade areas dominated by species with dense canopies. In New Zealand, dense beds of canopy-forming seaweeds dominate the intertidal-subtidal margin. One of the major seaweeds in this zone is the fucoid *C. maschalocarpum*. This species a major habitat-forming species of low shores around much of the coast of New Zealand and is particularly effective at preventing recruitment of conspecifics and other species because of its dense canopy (Schiel 1988). For *U. pinnatifida* to invade areas dominated by this species, it must have the ability to recruit rapidly and persist following a disturbance within these habitats. This must be done in competition with native species, which also have strategies to rapidly colonise gaps. It is therefore possible that the community of native species along the low intertidal zone coastline of New Zealand may have considerable inertia to disturbance and resilience when canopy disturbance does occur.

In this study, I examine the ability of *U. pinnatifida* to invade areas of the low intertidal dominated by the native *C. maschalocarpum* and use different sized canopy disturbances to mimic differences in disturbance intensity. The three main inter-specific hypotheses tested were that large areas of disturbed *C. maschalocarpum* canopy would be more susceptible to the invasion of *U. pinnatifida*;

smaller disturbed areas would recover more quickly than larger disturbed areas thus preventing further invasions; and the presence of coralline turf under the canopy facilitates *U. pinnatifida* recruitment. Further experiments examining intra-specific effects of *U. pinnatifida* canopy were done to determine if mature or immature conspecifics would inhibit recruitment.

## 4.2 Methods

The canopy removal experiments are divided into 3 experiments outlined in Table 4.1. The first experiment involved the removal of different sized areas of *C. maschalocarpum* canopy to determine the effects of these factors on recruitment and establishment of *U. pinnatifida*. The second experiment tested the effect of coralline turf and *C. maschalocarpum* canopy on the recruitment and establishment of *U. pinnatifida* at different temporal scales. The third experiment examined the effect of *U. pinnatifida* canopy on the recruitment of conspecifics over different temporal and spatial scales.

Throughout this study, recruitment of *Undaria pinnatifida* refers to new plants < 50 mm in length. New recruits were mapped within treatments and then tagged using Dymo™ tape as described in Chapter 2 (Section 2.2.1). This was done to ensure that new recruits were not confused with the previous months recruits. Note that “new plants” are readily distinguished from older plants that have been damaged and are <50 mm in length.

Table 4.1: Experimental designs for experiments done in sections 4.2.1, 4.2.2 and 4.2.3. “±*C.m.*” = presence/absence of *C. maschalocarpum*, “±T” = presence/absence of coralline turf, “±*U.p.*” = presence/absence of *U. pinnatifida*, “Mat.” = mature plants, “Imm.” = immature plants, RB = Rapaki Bay, MB = Moeraki Beach. N in bold = total number of treatments.

Expt.	Design		n	Site	Dates of canopy removal	Duration (months)	Size (cm)	Hypothesis
1	+ <i>C.m.</i> 5x5	- <i>C.m.</i> 5x5	4	RB	Aug 01	12	5x5	1. Large areas of <i>C.m.</i> canopy removal would be more susceptible to invasion by <i>U.p.</i> than small areas of canopy removal.
	+ <i>C.m.</i> 25x25	- <i>C.m.</i> 25x25					25x25	
	+ <i>C.m.</i> 50x50	- <i>C.m.</i> 50x50					50x50	
			24					
2	+ <i>C.m.</i> +T	- <i>C.m.</i> +T	5	RB	Mar 02	4	25x25	2. The presence of coralline turf underneath a <i>C.m.</i> canopy would facilitate recruitment of <i>U.p.</i> after canopy removal.
	+ <i>C.m.</i> -T	- <i>C.m.</i> -T			Jul 02			
			40					
3	+ <i>U.p.</i>	- <i>U.p.</i>	5	RB	Jul 01	3	50x50	3. Removal of conspecific canopy would result in recruitment of <i>U.p.</i> regardless of timing of canopy removal.
					Aug 01			
			30		Sep 01			
	+ <i>U.p.</i>	- <i>U.p.</i>	5	RB	Jun 02	3	50x50	
					Jul 02			
				MB	Jun 02			
			20		Jul 02			
	+ <i>U.p.</i> Mat.	- <i>U.p.</i> Mat	5	RB	Aug 02	3	50x50	4. Recruitment of <i>U.p.</i> would be greater in areas previously occupied by mature plants.
	+ <i>U.p.</i> Imm	- <i>U.p.</i> Imm		MB				
			40					

#### 4.2.1 Effects of inter-specific canopy and clearance size on recruitment

##### Hypothesis 1

To test the effects of size of *C. maschalocarpum* canopy disturbance on the ability of *U. pinnatifida* to recruit, a once only canopy removal experiment within the *C. maschalocarpum* band along the low shore at Rapaki Bay was done. Three treatments sizes were used covering all combinations of +canopy and -canopy with 4 replicates of each (Table 4.1, Expt. 1). Treatments were placed randomly and each corner was marked with a numbered nylon Ramset™ bolt drilled into the rock. Prior monitoring ensured that before treatment manipulations there was at least 95 % cover of *C. maschalocarpum* cover. All *C. maschalocarpum* plants were removed by cutting just above the base of the holdfast. This was to ensure that the surrounding

substratum was not disturbed. Treatments were at least 1 m apart to ensure independence. *Undaria pinnatifida* and *C. maschalocarpum* recruits were counted and their percent cover measured. *Carpophyllum maschalocarpum* recruited in particularly high numbers and subsequent mapping of individual plants proved impossible. Data were analysed using MANOVA (Statistica 6™). Count data were log transformed to meet the assumption of homogeneity of variance.

#### **4.2.2 Effects of inter-specific canopy and coralline turf on recruitment**

##### *Hypothesis 2*

To test the effects of canopy and the presence of coralline turf on the recruitment of *U. pinnatifida* a once-only canopy removal and turf removal experiment was done within the *C. maschalocarpum* habitat at Rapaki Bay. The experiment was done in March 2002 and repeated again in July 2002. The experiment consisted of a replicated (n=5) 2 x 2 factorial design with all combinations of treatments of canopy and canopy removal and turf and turf removal (Table 4.1, Expt. 2a). Treatment areas were placed randomly and consisted of 25 x 25 cm areas marked with a numbered nylon Ramset™ bolt drilled into the rock at each corner. Prior monitoring ensured that before treatment manipulations there was at least 95 % *C. maschalocarpum* cover and 80 % of coralline turf. Treatments were at least 50 cm apart and although this was not ideal, lack of suitable working area prevented further dispersion of treatments. In clearance treatments, all *C. maschalocarpum* plants were removed by cutting just above the base of the holdfast. Removal quadrats were scraped to ensure all organisms and propagules were eliminated. This also removed all crevices in the substratum. Treatments for both experiments were monitored monthly for 6 months. The number of *U. pinnatifida* and *C. maschalocarpum* recruits were counted and their length measured.

### 4.2.3 Effects of intra-specific canopy on recruitment

#### *Hypothesis 3*

To test the effects of *U. pinnatifida* canopy on recruitment of conspecifics, a series of canopy removal experiments were done within stands of *U. pinnatifida* at Rapaki Bay and Moeraki Beach (Expt. 3, hypothesis 3, Table 4.1). These experiments had two treatments, canopy removal and canopy left intact (n=5) and were installed within the *U. pinnatifida* zone. Treatment areas were placed randomly and consisted of 50 x 50 cm areas marked with a numbered nylon Ramset™ bolt drilled into the rock at each corner. Treatments were at least 1 m apart to ensure independence. The first experiment (hypothesis 3, Table 4.1) was done at Rapaki Bay between July 2001 and September 2001. Treatments were installed during July, August and September 2001. The experiment was repeated again during June and July 2002 at Rapaki Bay and Moeraki Beach, respectively (hypothesis 3, Table 4.1).

#### *Hypothesis 4*

A further experiment was initiated during August 2002 at Rapaki Bay and Moeraki Beach to test the effects of removal of mature versus immature canopy plants on recruitment of *U. pinnatifida* (hypothesis 4 Table 4.1). At both sites four treatments (n=5) were installed; removal of immature canopy, removal of mature canopy, both immature and mature canopies left intact (hypothesis 4 Table 4.1).

For each experimental treatment, there was at least 95 % canopy cover prior to manipulation. Prior to canopy removal, plants were counted and analysed (one-way ANOVA) to ensure an even abundance between treatment and replicates (no differences were found ( $p < 0.05$ )). Canopy removal was done by cutting plants above the holdfast so the surrounding substratum was not disturbed. Recruits (<50 mm in total length) were counted for three months from the initiation of the experiments. Longer sampling could not be achieved due to most plants in the controls senescing and reducing the amount of canopy. Data were log-transformed to meet the assumptions of homogeneity of variance and analysed using ANOVA (Statistica 6™).

### 4.3 Results

#### 4.3.1 Effects of inter-specific canopy and clearance size on recruitment

##### Recruitment

There was a significantly greater number of new *C. maschalocarpum* recruits than *U. pinnatifida* recruits in all sized treatments after 12 months (Fig. 4.1, Table 4.2) but there were no differences in individual species number across different sized clearances (Table 4.3) The controls (+canopy) had no recruitment of either species during the entire experiment so were not included in the analysis. *Carpophyllum maschalocarpum* recruits were considerably smaller (<10 mm) than *U. pinnatifida* recruits (<50 mm).

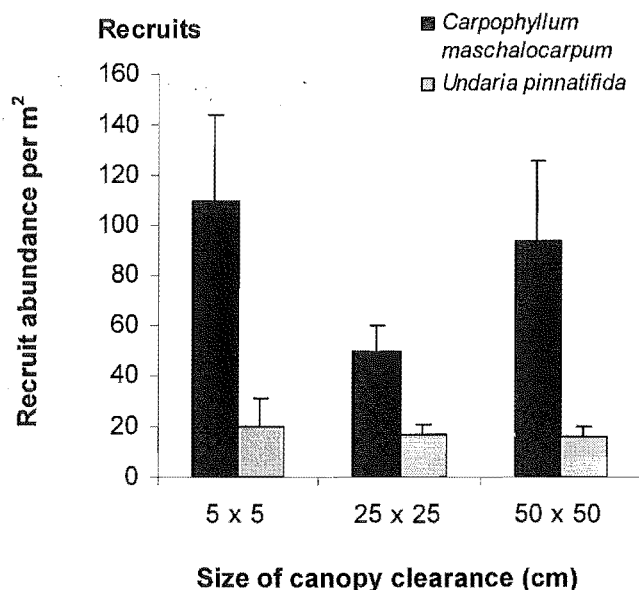


Figure 4.1: Mean cumulative recruit abundance (number per m<sup>2</sup>) (+1 S.E.) of *C. maschalocarpum* and *U. pinnatifida* after 12 months following 5 x 5, 25 x 25 and 50 x 50 cm *C. maschalocarpum* canopy clearances at Rapaki Bay. Clearances were initiated during August 2001.

Table 4.2: Mean cumulative number ( $\pm 1$  S.E.) of recruits of *C. maschalocarpum* and *U. pinnatifida* recruits observed (counts) and standardised to 1 m<sup>2</sup> in different sized canopy gaps between September 2001 and August 2002. ANOVA (one way) results are given in the right hand column (a,b, indicate results of Tukey's HSD test; values with the same letter were not significantly different at  $p < 0.05$ ).

Gap Size	<i>Carpophyllum maschalocarpum</i>		<i>Undaria pinnatifida</i>		Anova
	Counts	Standardised	Count	Standardised	
5 x 5	2.75 $\pm$ 0.85	110 $\pm$ 34.15 a	0.5 $\pm$ 0.28	20 $\pm$ 11.54 b	$F_{(1,6)} = 6.29$ $p < 0.05^*$
25 x 25	31.1 $\pm$ 6.48	49.63 $\pm$ 10.3 a	10.75 $\pm$ 2.01	17.2 $\pm$ 3.22 b	$F_{(1,6)} = 8.90$ $p < 0.05^*$
50 x 50	79.5 $\pm$ 19.78	93.9 $\pm$ 31.49 a	14.25 $\pm$ 3.27	16.2 $\pm$ 4.05 b	$F_{(1,6)} = 17.93$ $p < 0.01^{**}$

Table 4.3: Results of MANOVA on cumulative recruit abundance (standardised to 1m<sup>2</sup>) of *C. maschalocarpum* and *U. pinnatifida* after 12 months from initiation of a *C. maschalocarpum* canopy clearance (August 2001) at Rapaki Bay. Independent factor is clearance size (= 5 x 5, 25 x 25, 50 x 50 cm). Data were not transformed. Cochran's test was not significant.

Effect	df	Wilks Lamda	Rao's R	p
Gap size	2,4	0.6065	1.14	0.3748

The patterns of recruitment of *C. maschalocarpum* contrasted to those of *Undaria pinnatifida*. Initially, the removal of the *C. maschalocarpum* canopy at a single time resulted in recruitment of *U. pinnatifida* within one month in all cleared size treatments (Fig. 4.2). Subsequent recruitment of *U. pinnatifida* during October and November was low and only occurred in the medium (25 x 25 cm) and largest (50 x 50 cm) gaps (Fig. 4.2). No *U. pinnatifida* recruitment occurred during the summer months between November 2001 and March 2002 (Fig. 4.2). During April and May 2002, small numbers of recruits were found in the medium (25 x 25 cm) and largest (50 x 50 cm) gaps. No further *U. pinnatifida* recruitment occurred. In contrast, *C. maschalocarpum* recruited in vast numbers between December 2002 and February 2002 in all clearance size treatments. This coincided with the senescence of post reproductive *U. pinnatifida* plants.

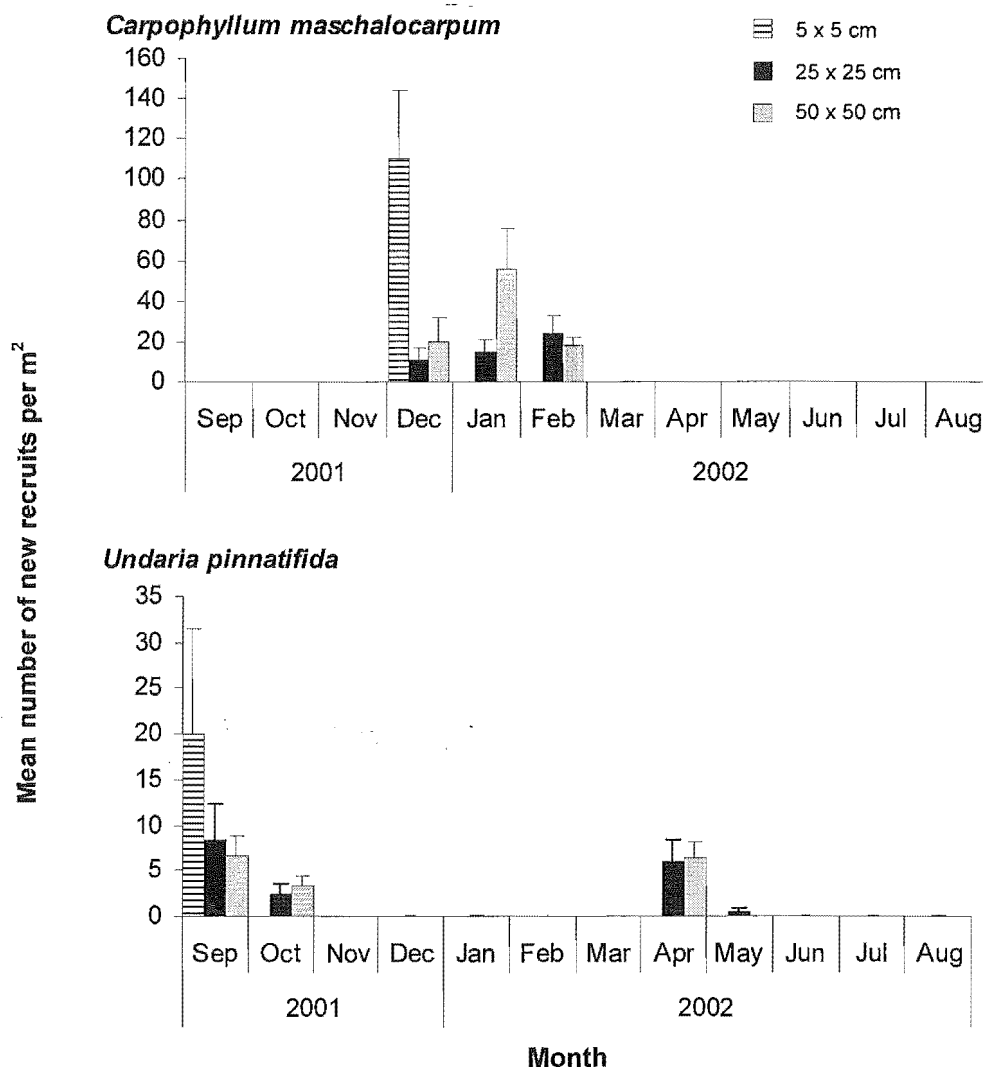


Figure 4.2: Mean number of new recruits of *C. maschalocarpum* and *U. pinnatifida* appearing in each sampling period (number per m<sup>2</sup>) ( $\pm 1$  S.E.) within different sized canopy clearance treatments between September 2001 and August 2002 at Rapaki Bay. Canopies were cleared in August 2001. Treatments refer to sizes of canopy gaps in cm.

#### Canopy recovery

After 12 months, a progressive decline in *C. maschalocarpum* canopy was observed between size treatments whereas an increase in *U. pinnatifida* canopy had occurred (Fig. 4.3). The differences can be attributed to the relatively slower growth rates of *C. maschalocarpum* recruits over the 12 months. Across all gap size treatments plant size differed significantly ( $F_{(1,32)} = 139.86$ ,  $p < 0.01$ ). *Carpophyllum maschalocarpum* plants were  $58.33 \pm 1.71$  mm in length after 12 months whereas *U. pinnatifida* were  $410.53 \pm 40.47$  mm in length.



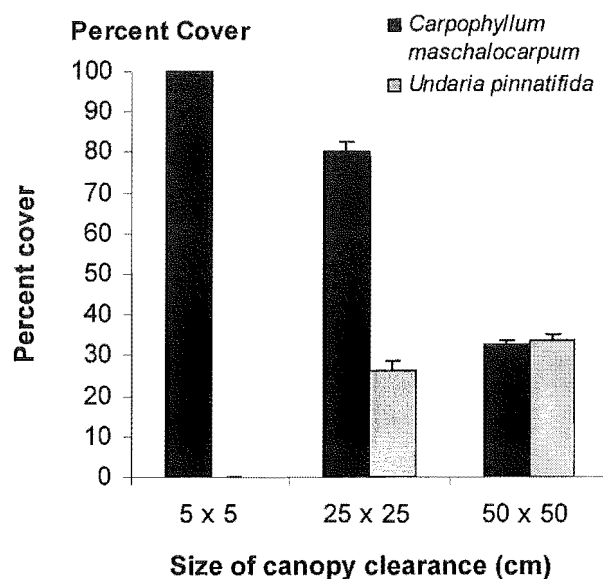


Figure 4.3: Mean percent cover (+1 S.E.) of *C. maschalocarpum* and *U. pinnatifida* after 12 months following 5 x 5, 25 x 25 and 50 x 50 cm *C. maschalocarpum* canopy clearances at Rapaki Bay. The experiment was initiated during August 2001.

By August 2002, the smallest (5 x 5 cm) gaps had reverted to original levels of canopy cover with no *U. pinnatifida* present (Fig. 4.3). The medium (25 x 25 cm) gaps had almost 80% recovery, however *U. pinnatifida* plants had formed a canopy which covered the remaining area. In contrast, the largest (50 x 50 cm) gaps resulted in poor levels of recovery of *C. maschalocarpum* (<35%) (Fig. 4.3). The differences in canopy formation between the medium (25 x 25 cm) and large (50 x 50 cm) gaps resulted in significant differences in recovery of gap size for both species (Table 4.4) (due to lack of variation in canopy cover scores, the 5 x 5 cm gaps in this treatment were removed from the analysis). The controls (+canopy) remained unchanged throughout the experiment.

Table 4.4: Results of MANOVA on percentage cover of *C. maschalocarpum* and *U. pinnatifida* plants after 12 months from initiation of a *C. maschalocarpum* canopy clearance (August 2001) at Rapaki Bay. Independent factor is size (= 25 x 25, 50 x 50). Data were arc-sine transformed. Cochran's test was not significant.

Effect	df	Wilks Lamda	Rao's R	p
Gap size	1,5	0.0099	248.02	p<0.01

Patterns of recovery of the *C. maschalocarpum* canopy were different amongst the different gap size treatments. Recovery was quickest in the smallest (5 x 5 cm) gaps (Fig. 4.4). Complete recovery took almost 6 months from the time of clearance and was the result of new recruits and surrounding plants filling the gaps (Fig. 4.4). In contrast, recovery was much slower in the medium sized gaps (25 x 25 cm) and largest gaps (50 x 50 cm) and full recovery to pre-experimental conditions had not occurred by August 2002 (Fig. 4.4). Most *C. maschalocarpum* plants observed during the experiment grew slowly and rarely exceeded 50 mm in length. However, due to the prostrate form of recruits they were able to "spread" over the clearances.

*U. pinnatifida* canopy showed a cyclical pattern with peaks of canopy cover occurring during spring (September- December 2001) and winter (June- August 2002) followed by periods of degeneration in all gap size treatments in summer (Fig. 4.4). Rapid growth of *U. pinnatifida* recruits in the medium gaps (25 x 25 cm) resulted in almost complete coverage by plants (> 600 mm in length) during November 2001. This was at a period when *C. maschalocarpum* plants were absent (Fig. 4.4). During the same period, plants in the larger gaps (50 x 50 cm) were of similar length to those in the medium gaps, but lower *U. pinnatifida* canopy coverage occurred (40%) (Fig. 4.4). Similar patterns of *U. pinnatifida* coverage were observed for both the medium (25 x 25 cm) and large (50 x 50 cm) gaps between March and August 2002 (Fig. 4.4).

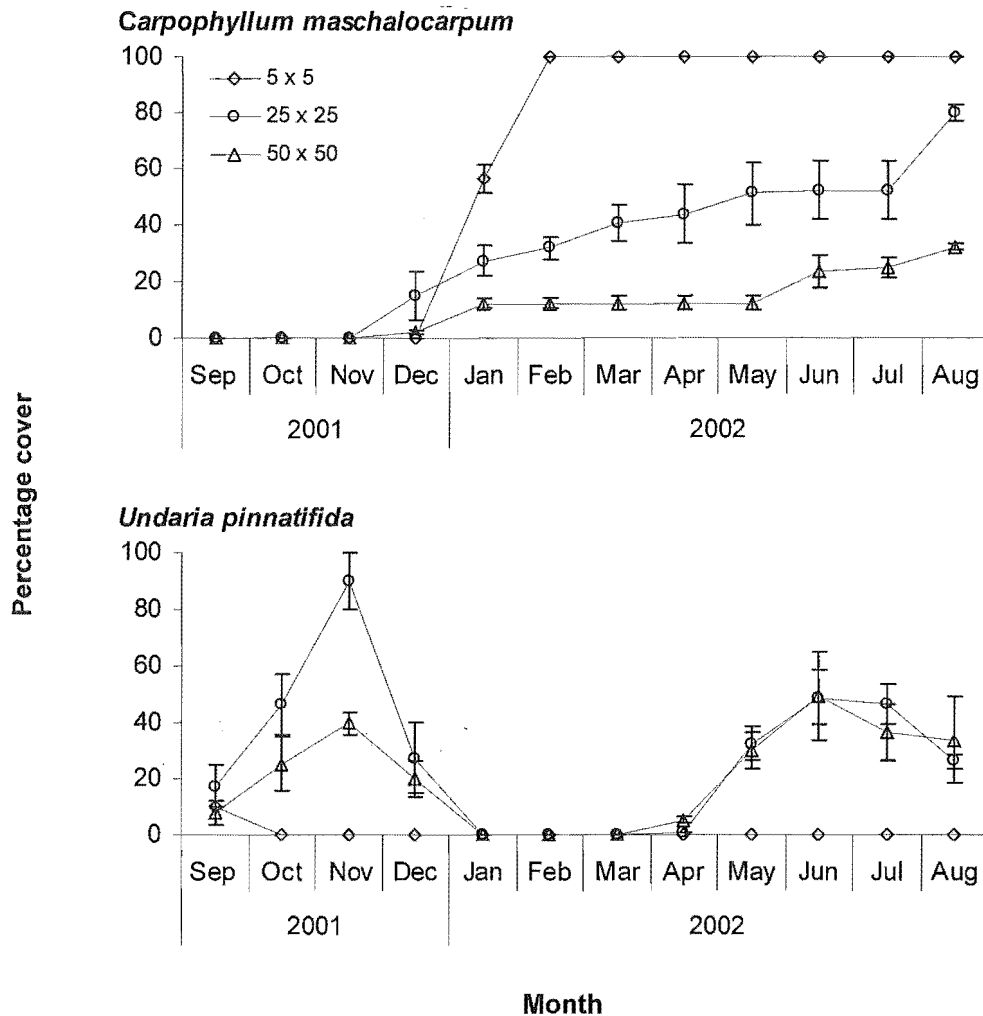


Figure 4.4: Mean percentage cover ( $\pm 1$  S.E.) of *C. maschalocarpum* and *U. pinnatifida* plants each month within different sized canopy clearance treatments between September 2001 and August 2002 at Rapaki Bay. Canopies were cleared in August 2001. Numbers on treatments refer to sizes of canopy gaps in cm.

#### Substratum cover

Prior to initiation of the experiment the substratum of the small (5 x 5 cm) sized treatments were covered with a mixture of bare space, coralline turfs and *C. maschalocarpum* holdfasts (Fig. 4.5). The medium (25 x 25 cm) and larger (50 x 50 cm) treatments were covered with a mixture of coralline turfs, bare space, bryozoans and holdfasts (Fig. 4.5). In most treatments, many of the holdfasts of *C. maschalocarpum* were attached to the bare substrata, but were entwined amongst the turf and bryozoans.

An increase in the amount of coralline turf and a decrease in the amount of holdfast and bare space was observed in the small (5 x 5 cm) gaps after 12 months (Fig. 4.5). Substrata composition within the medium (25 x 25 cm) gaps did not differ after 12 months. An increase in coralline turf and a decrease in bare space was observed in the medium controls (Fig. 4.5). Similarly, no change was observed in the large 50 x 50 cm) gaps but a decrease was observed in the amount of bare space in the controls after 12 months. Within each treatment, most *U. pinnatifida* recruits occurred within short coralline turfs that remained on the substratum whereas *C. maschalocarpum* recruited onto bare surfaces.

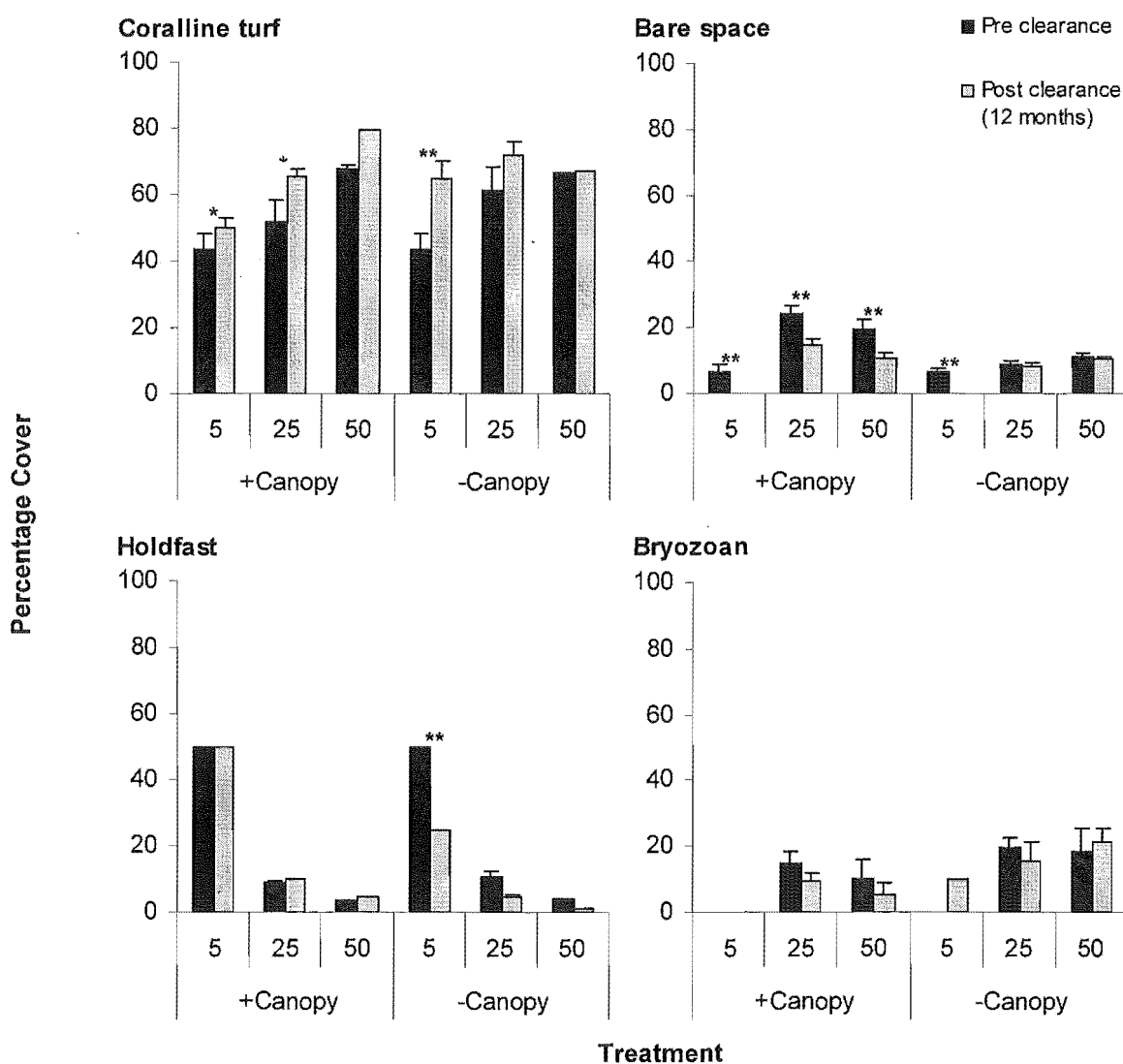


Figure 4.5: Mean percentage cover (+1 S.E.) of coralline turf, bare space, *C. maschalocarpum* holdfasts and bryozoans within different sized canopy treatments before the initiation of clearances (August 2001) and 12 months later (August 2002) at Rapaki Bay. Numbers on the x axis represent treatment sizes (5 x 5 cm, 25 x 25 cm, 50 x 50 cm). \* ( $p < 0.05$ ), \*\* ( $p < 0.01$ ) significant result of one way ANOVA. Cochran's tests were not significant.

#### 4.3.2 Effects of inter-specific canopy and coralline turf on recruitment

All *U. pinnatifida* recruits were found in the -canopy +turf treatment for experiments initiated during March and July 2002 (Fig. 4.6). For the March clearances, recruitment occurred the following month and continued until June 2002 (Fig. 4.6). Recruitment in the July clearances did not occur until September and October 2002, two months after initiation of the experiment. The cumulative number of recruits was significantly greater for the March clearances than the July clearances ( $F_{(1,6)}=9.85$ ,  $p<0.05$ ), which might simply reflect the longer recruitment period observed in March (3 months) than in July (2 months) (Fig. 4.6). In the -canopy +turf treatment, rapid growth of *U. pinnatifida* plants resulted in high percentages of canopy coverage after 4 months in both the March and July experiments (Fig. 4.7).

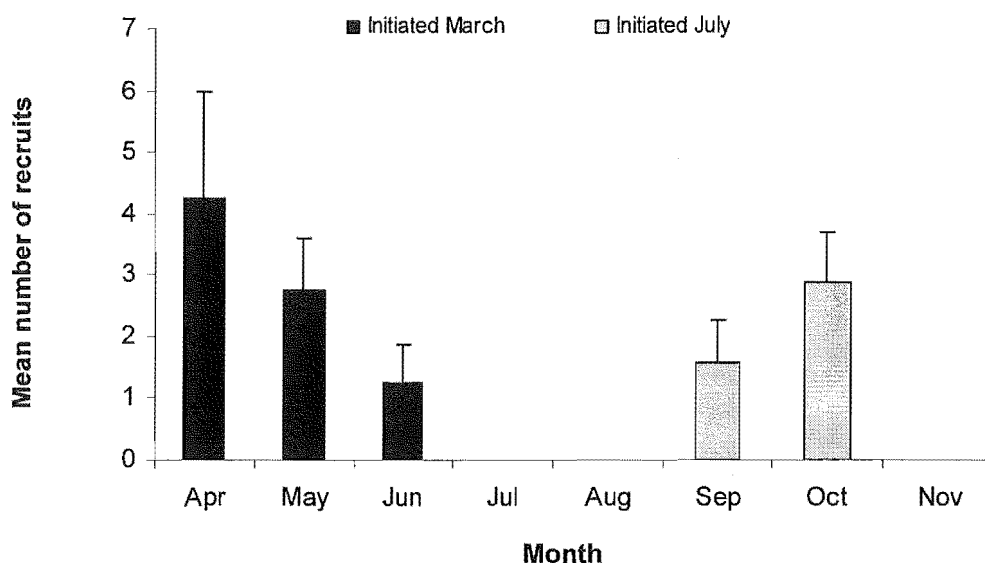


Figure 4.6: Mean number ( $\pm 1$  S.E.) of new *U. pinnatifida* recruits per 25 x 25 cm found within the -canopy +turf treatments at Rapaki Bay during 2002. Black bars indicate the experiment initiated during March 2002. Grey bars indicate the experiment initiated during July 2002.

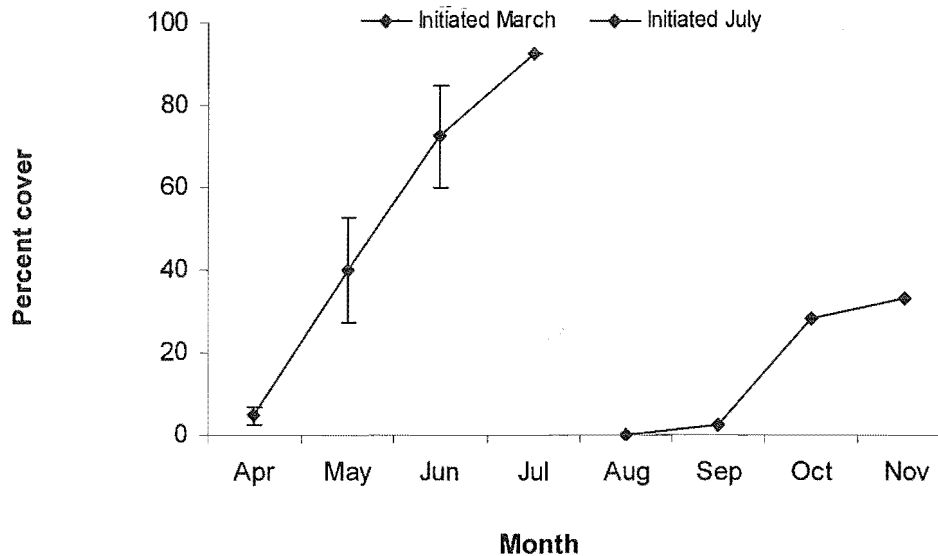


Figure 4.7: Mean percent cover ( $\pm 1$  S.E.) of *U. pinnatifida* per 25 x 25 cm found within the – canopy +turf treatments at Rapaki Bay during 2002.

#### 4.3.3 Effects of intra-specific canopy on recruitment

##### *The effects of timing of canopy removal on recruitment*

A clear canopy removal effect was observed for all months in which the experiment was initiated. No recruitment was observed in the controls and only one recruitment episode was observed in each of the treatments (Fig. 4.8). The majority of recruits occurred either within the holdfast of removed plants or within ~50 mm of the removed plant. For the experiments initiated during July and August, recruits were found in September (Fig. 4.8). Because of the prevalence of zeroes in the control data, no statistical analyses were done.

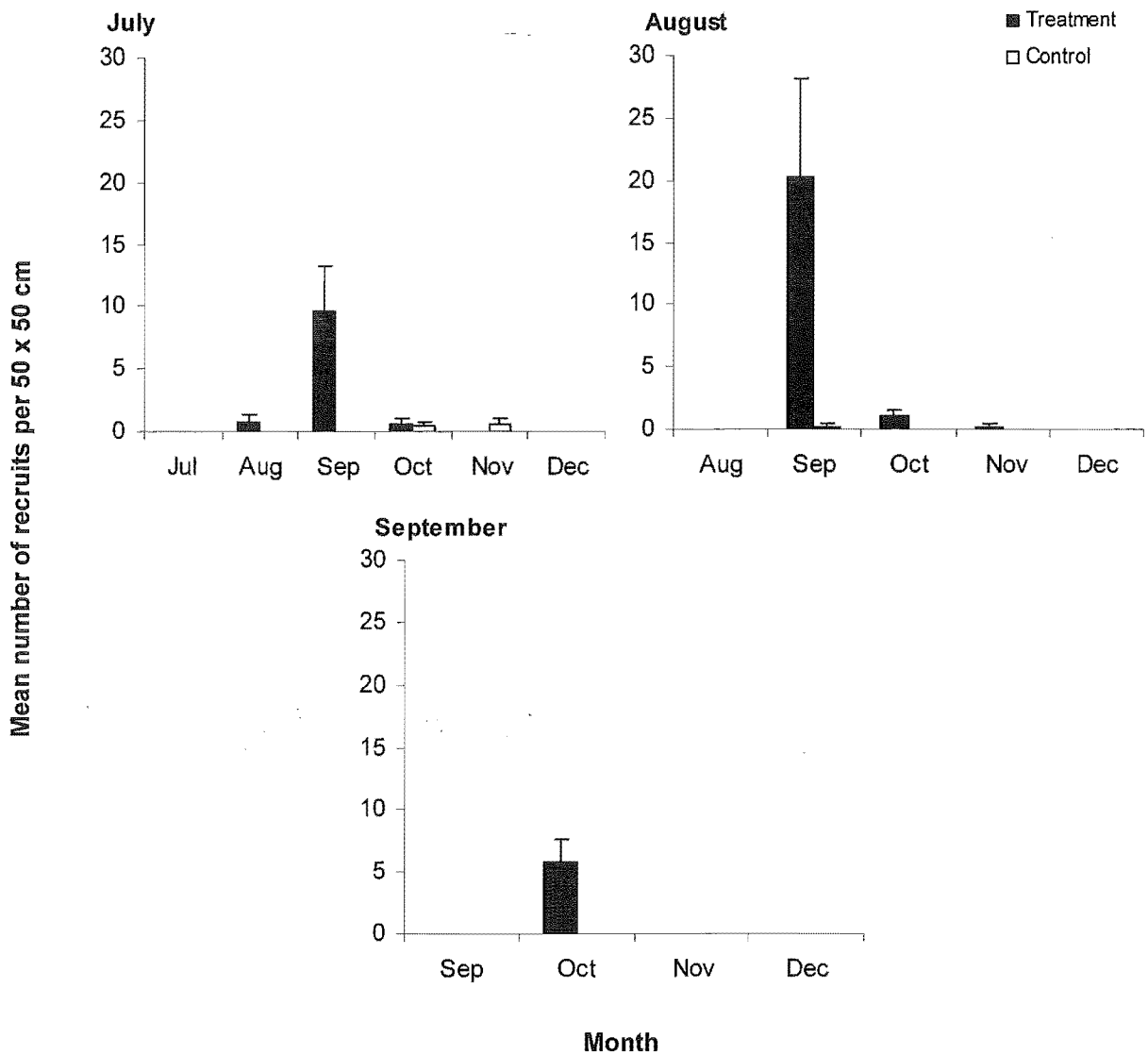


Figure 4.8: Mean number ( $\pm 1$  S.E.) of new *U. pinnatifida* recruits after removal of conspecific canopy during July, August and September 2001 at Rapaki Bay. Control = *U. pinnatifida* canopy, Removal = *U. pinnatifida* canopy removed.

Recruitment, although at low levels, occurred at both Rapaki Bay and Moeraki Beach immediately after the initiation of the experiment within the canopy removal treatment (Fig. 4.9). There was a significant effect of canopy removal on the cumulative number of recruits at Rapaki Bay and Moeraki Beach. However, the timing of canopy removal or the site in which it was done were not significant (Table 4.5).

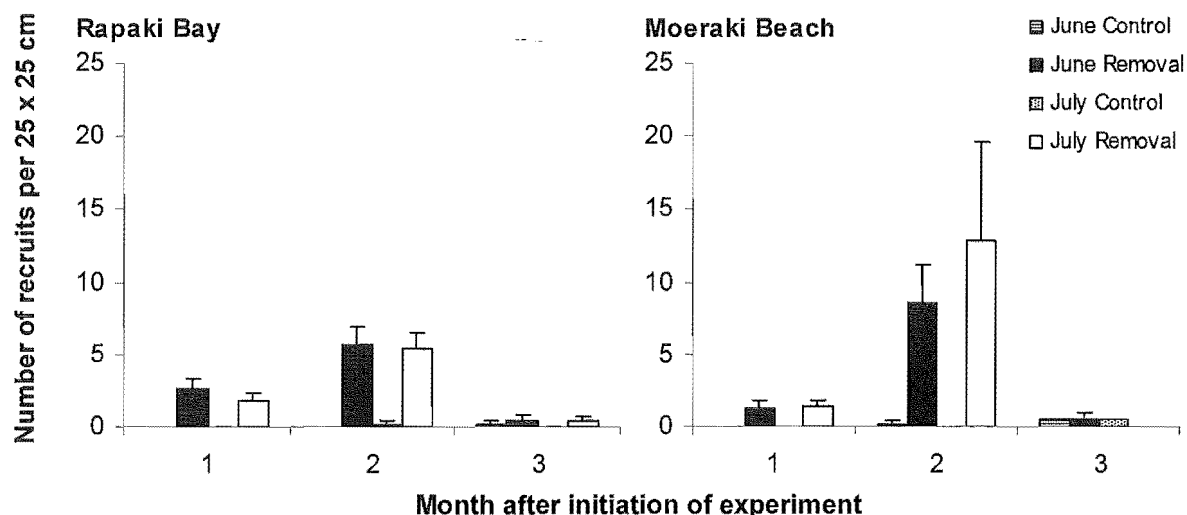


Figure 4.9: Mean number (+1 S.E.) of new *U. pinnatifida* recruits after removal of conspecific canopy during June and July 2002 at Rapaki Bay and Moeraki Beach. Control = *U. pinnatifida* canopy, Removal = *U. pinnatifida* canopy removed.

Table 4.5: Results of three-way ANOVA on the effect of site, timing of canopy removal and presence of canopy on the cumulative number of *U. pinnatifida* recruits during 2002. Independent factors are site (=Rapaki Bay, Moeraki Beach), time (=June, July), canopy (=+canopy, -canopy). Treatment sizes were (50 x 50 cm). Data were log-transformed. Cochran's test was not significant.

Effect	df	MS	F	p
Site	1	0.097	0.248	0.622
Time	1	0.001	0.002	0.962
Canopy	1	39.225	100.542	p<0.01
Site x Time	1	0.012	0.03	0.864
Site x Canopy	1	0.049	0.124	0.727
Time x Canopy	1	0.004	0.01	0.922
Site x Time x canopy	1	0.0003	0.001	0.979
Error	32	0.390		

#### *Immature and mature canopy effects*

There was a significant treatment effect at both Rapaki Bay (no plants recruited into the control) and Moeraki Beach ( $F_{(2,6)}=26.06$ ,  $p<0.01$ ), with more recruits occurring in areas when canopies were removed (Fig. 4.10). Subsequent analysis was only done on the removal treatments for the cumulative number of recruits over three months. There were significant differences between the two sites with cumulative recruit



number greater at Rapaki Bay within immature and mature treatments than at Moeraki Beach (Table 4.6).

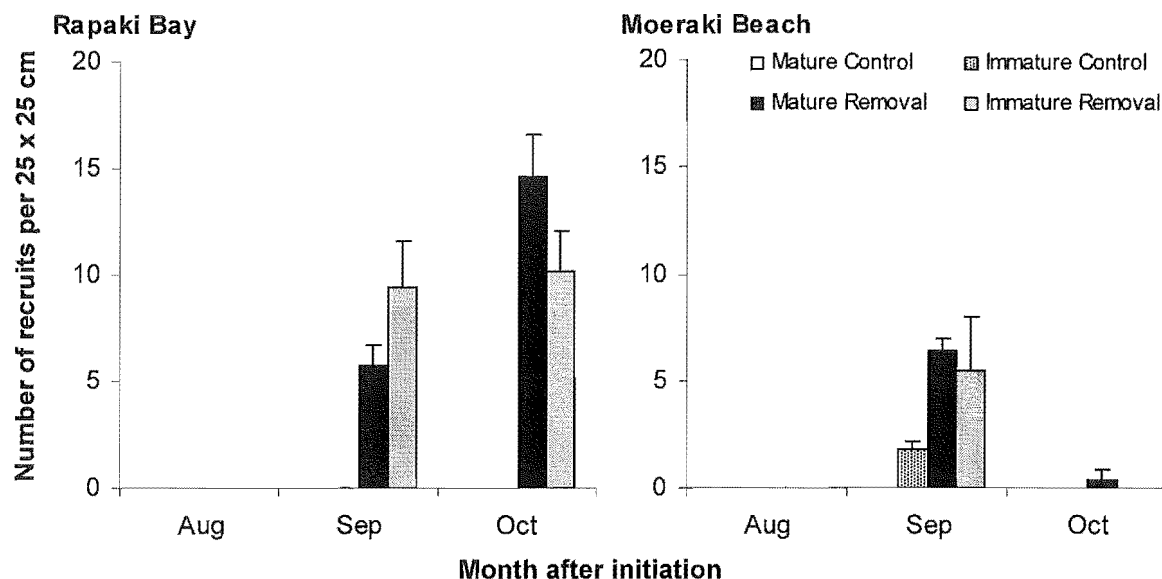


Figure 4.10: Mean number (+1 S.E.) of new *U. pinnatifida* recruits after removal of conspecific mature and immature canopies Rapaki Bay and Moeraki Beach. Controls = *U. pinnatifida* canopy, Removals = *U. pinnatifida* canopy removed.

Table 4.6: Results of two-way ANOVA on the effects of site and stage on the cumulative number of *U. pinnatifida* recruits after *U. pinnatifida* canopy removal. Independent factors are site (=Rapaki Bay, Moeraki Beach), stage (=mature, immature). Data were log-transformed. Cochran's test was not significant.

Effect	df	MS	F	p
Site	1	6.216	156.264	p<0.01
Stage	1	0.074	1.867	0.191
Site x Stage	1	0.041	1.048	0.321
Error	16	0.039		

#### 4.4 Discussion

##### *Mechanisms of recruitment*

Removal of both *C. maschalocarpum* and *U. pinnatifida* canopies in this study resulted in recruitment of *U. pinnatifida*, supporting the hypothesis that the canopy is responsible for limiting the density of recruits in stands of both species. The mechanism by which the canopy inhibits recruitment was not investigated, but most studies involving canopy removals attribute enhanced recruitment following a canopy

removal to increased light levels (Reed and Foster 1984; Santelices and Ojeda 1984; Jenkins *et al.* 1999a&b). Numerous subtidal studies have shown that low light levels caused by macroalgal canopies can inhibit recruitment of both conspecifics and other species of algae (Kain 1979; Dayton *et al.* 1984; Reed and Foster 1984; Schiel 1988; Kennelly 1987a). For example, Reed and Foster (1984) found that the removal of *Macrocystis pyrifera* and *Pterygophora californica* canopies within sheltered areas resulted in the recruitment of both original canopy species and the annual kelp *Desmarestia ligulata* (Reed and Foster 1984). The recruitment of these species was suggested to be the result of a 5 % increase in light levels reaching the bottom following canopy removal.

However, studies within the intertidal, which is a comparatively high light environment, have shown a number of other factors could be responsible for increased recruitment following canopy removal (Brawley and Johnson 1991). For example, canopies of *Pelvetia fastigata* negatively affected conspecific propagules by fronds scouring the substrata. In areas removed of canopy, recruits were found in high numbers (Brawley and Johnson 1991). Alternatively, the simultaneous absence of grazers after canopy removal may have occurred. In my study, few macroinvertebrate grazers existed beneath the canopy. However, within the holdfasts and surrounding coralline turfs a number of mesograzers, such as amphipods and copepods, were found. The possibility that the reduction in canopy cover may have resulted in fewer mesograzers cannot be discounted.

Although these factors may be important in inhibiting recruitment in some intertidal species, in my study low light was possibly inhibiting recruitment of *U. pinnatifida* for a number of reasons. First, the high densities and coverage of *U. pinnatifida* plants when exposed during low tide usually covered 100 % of the substrata and was likely to reduce light levels. Similarly, *C. maschalocarpum* forms dense intertwined canopies that drape over the substrata and when exposed during low tide are likely to reduce light levels. Second, continual re-suspension of sediments from the incoming and outgoing tides meant that the surrounding water was often turbid and light penetration was poor. Third, it has been suggested that the strain of *U. pinnatifida* introduced to New Zealand is a cultivated strain from Japan that has been

selected for growing on secondary substrata and requires higher light requirements for development and growth than wild populations of *U. pinnatifida* in Japan (Stuart 1997).

*U. pinnatifida* requires high saturating levels of PFD (Photon Flux Density) for gametogenesis to occur, but more importantly a specific blue quantum dose is required (Stuart 1997). Stuart (1997) found that a blue quantum dose of between 3 and 3.5 mol. m<sup>-2</sup> and PFD of 20-30  $\mu\text{mol}^{-2}\text{s}^{-1}$  was required for gametogenesis. These levels are much higher than what is required for most perennial laminarians such as *M. pyrifera* (between 1.1 and 2.6 mol. m<sup>-2</sup> blue quantum dose) but are similar to opportunistic laminarians such as *Nereocystis leutkeana* (PFD 20-40  $\mu\text{mol}^{-2}\text{s}^{-1}$ ) (Stuart 1997). Increased light levels after canopy removal may initiate growth of settled propagules of *U. pinnatifida*, however further experiments are required to determine the exact mechanism(s) behind increased levels of recruitment following canopy removal.

### Seed bank

The rapid recruitment of *U. pinnatifida* after canopy removal suggests that the appearance of recruits was either reliant on a continual supply of propagules or the presence of pre-existing propagules within a "seed bank" that developed following canopy clearance. Opportunistic species such as *Enteromorpha* spp. and filamentous brown algae rely on a continual supply of propagules to colonise areas (Hruby and Norton 1979). Once propagules have settled, recruits may take about 1-2 months to appear (Hruby and Norton 1979; Kennelly 1987a). Alternatively, gametophytes may provide the means of surviving unfavourable recruitment conditions, particularly low light conditions (Hoffmann and Santelices 1991; Edwards 2000). For example, in *Laminaria hyperborea*, gametophytes grown under a variety of light conditions had different germination rates (Kain 1964). Gametophytes grown in darkness for 10 days then subjected to 5.2  $\mu\text{g.cal/cm}^2\text{sec}$ . 12:12 L:D became fertile after 130 days but survival of female gametophytes was very low (~9%) (Kain 1964). Kimura and Foster (1984) suggested dormant juveniles of *P. californica* and *M. pyrifera* are probably available throughout the year and can colonise immediately after a disturbance to the surrounding canopy. This has been supported by recent

laboratory experiments that have shown embryonic *M. pyrifera* sporophytes can delay recruitment under low light and nutrient conditions (Kinlan *et al.* 2003).

Embryonic sporophytes and not gametophytes may be responsible for delayed recruitment in *U. pinnatifida* for a number of reasons. First, if reproductive adults had released spores simultaneously with canopy clearance, then the period between spore release and appearance of visible recruits may be too long. Previous studies on *U. pinnatifida* have shown that the time taken from spore release to gametophyte fertilisation is approximately 30- 40 days, with increased development times occurring at temperatures less than 16 °C (Stuart 1997). Further development to recruit size (i.e. from 0.2 mm to 10- 50 mm in length) would have had to occur within 1 month. Second, if dormant gametophytes were present, then the increased availability of light would have to initiate fertilisation within a very short period. Kain (1964) showed that the *L. hyperborea* gametophytes subjected to 10 days darkness then placed in high light conditions (220  $\mu\text{g.cal/cm}^2\text{sec}$ . 12:12 L:D) at 10°C became fertile at approximately 21 days. If *U. pinnatifida* gametophytes developed at a similar rate to that of *L. hyperborea*, then rapid growth of embryonic sporophytes would have had to occur for recruits to appear within two months. Alternatively, embryonic sporophytes of *U. pinnatifida* may be present underneath canopies but growing at very slow rates. Increased light levels following canopy removal may increase growth rates resulting in recruitment 1- 2 months later. The ability of embryonic sporophytes of *U. pinnatifida* to delay recruitment may be an important mechanism to ensure propagule survival in sub-optimal conditions and ensure recruit success following episodic disturbances.

*U. pinnatifida* recruits appeared regardless of timing of intra-specific canopy removal in relation to reproductive season. This contrasts with previous results that have examined the timing of canopy removal in relation to reproduction. For example, Schiel (1988) reported that canopy removal experiments in *Ecklonia radiata*, *C. maschalocarpum*, *C. angustifolium* and *Sargassum sinclarii* produced similar results among species. If removals were done outside the reproductive season, a mixture of species including the original species recruited. In contrast, if removals were done during the reproductive season, then conspecific recruits appeared and dominated.

This suggests that recruitment largely depends on the reproductive periodicity of algae for these species (Schiel 1988). Timing of canopy disturbance was found to be important in the establishment of *U. pinnatifida* in subtidal areas of Tasmania (Valentine and Johnson 2003). *U. pinnatifida* recruited in higher densities in areas where the native canopy was removed immediately prior to the sporophyte growth season. In contrast, plots where the canopy was removed during the period of spore release resulted in low recruitment. In my study, the recruitment of *U. pinnatifida* occurred regardless of timing of canopy removal. This provides further evidence that a “seed bank” exists for *U. pinnatifida*, but also indicates that canopies have a very strong suppressive effect on recruits.

Coralline turfs, which appear essential to effective recruitment of *U. pinnatifida* in the intertidal zone, may facilitate the survival of “seed banks” through a number of possible mechanisms. First, coralline turfs may protect microscopic stages of *U. pinnatifida* from *C. maschalocarpum* fronds scouring the substratum. Previous studies have shown that fronds of canopy species can effectively remove recently settled propagules (Black 1974; Brawley and Johnson 1991). Much of the turf found under the *C. maschalocarpum* canopy was near the base of holdfasts and away from the tips of the fronds, so scouring may be ineffective at removing propagules that settle within the turf. Second, grazing by macroinvertebrates within areas cleared of coralline turf may have occurred (Vadas *et al.* 1992). Jenkins *et al.* (1999b) found that limpets were effective at grazing recruits of *Fucus serratus* on bare substrata, both outside and under canopies, but not within coralline algae that existed amongst the treatments. In my study, very few macroinvertebrate grazers were found with the *C. maschalocarpum* zone so their impact on *U. pinnatifida* recruitment may be negligible. The most likely explanation for the differences observed between treatments is that coralline turfs provide a microhabitat for microscopic stages and protect them from the physical stresses associated with exposure during low tide. Previous studies have shown that microhabitats, are important in providing refuges for algal propagules. For example, propagules of *Pelvetia fastigata* occupy distinct microhabitats within the intertidal that are thought to increase survival of early post settlement stages. When propagules are exposed outside of these microhabitats high mortality occurs (Brawley and Johnson 1991). It is possible that coralline turfs

may facilitate the survival of microscopic stages of *U. pinnatifida*, however the possibility that reproductive failure or poor dispersal of propagules may have occurred within other treatments cannot be ruled out (see Chapter 2).

The ability to suspend development during the microscopic stage is recognised as an adaptation of algae to survive conditions that are stressful to the macroscopic stage (Santelices 1990b). Furthermore, a “seed bank” may be the only strategy that competitively-inferior individuals have to ensure possible survival to reproduction (Creed *et al.* 1996). The “seed bank” of *U. pinnatifida* may be an important life history feature that allows it to establish, persist and encroach into new areas previously occupied by superior competitors.

### *Competition*

Removal of different-sized areas of *C. maschalocarpum* canopy resulted in contrasting patterns of canopy recovery after 12 months. In the smaller (5 x 5 cm) clearances, full recovery of the canopy occurred within 6 months. In contrast, the medium (25 x 25 cm) clearances recovered to about 80 % of its original canopy cover whereas the large (50 x 50 cm) clearances had about 30 % canopy recovery. *C. maschalocarpum* canopy removal resulted in the establishment of *U. pinnatifida* over a short period in all clearances, but the persistence only occurred in the larger (25 x 25 cm and 50 x 50 cm) clearances.

In a subtidal study in Tasmania, a 2 x 2 m reduction of the native algal canopy was found to be critical in the establishment of *U. pinnatifida*, while the presence of a stable native algal canopy inhibited invasion (Valentine and Johnson 2003). Over a period of two years, *U. pinnatifida* abundance declined significantly within the cleared treatments due to the recovery of native canopy-forming species. Although native canopies showed some resilience to disturbance, individual species resilience was poor. Species dominant prior to canopy removal showed little if any signs of recovery. Instead, recovery was dominated by canopy-forming species that were either rare or previously absent within the study areas (Valentine and Johnson 2003). Although only size of clearance (2 x 2 m) was used in Valentine and

Johnson's (2003) study results from my study suggest that gap size is important in the resilience of *C. maschalocarpum* to invasion by *U. pinnatifida*.

Results from my study contrast results from the few studies that have examined the effect of canopy gap size on the recruitment of macroalgae within the intertidal species. For example, Jenkins *et al.* (1999b) examined the effect of small (50 x 50 cm) and large (1 x 1 m) canopy clearances of the intertidal species *Fucus serratus* and found no significant effect of clearance size on canopy recovery. *Fucus serratus* canopy recovered to about 75 % of its original cover in 2 years through recruitment of juveniles (Jenkins *et al.* 1999b). However, limpet grazing had a significant effect on the re-establishment of *F. serratus* canopy (Jenkins *et al.* 1999b). The contrasting results between my study and Jenkins *et al.*'s (1999b) study suggest that different factors may be affecting recruitment of both species following canopy removal.

The ability to invade gaps may be attributed to the different morphological characteristics of the species. Schiel (1988) suggested that morphological differences between laminarians and fucaleans may allow laminarians to secure space more effectively. For example, the laminarian *Ecklonia radiata* has a considerably larger holdfast and can occupy more space than most fucalean holdfasts. Similarly, the holdfasts of *U. pinnatifida* are much larger than the holdfasts of *C. maschalocarpum* and therefore occupy more space. However, the annual nature of *U. pinnatifida* means that the holdfasts only occupy space for a limited period. *U. pinnatifida* holdfasts usually disappear prior to *C. maschalocarpum* reproduction.

Results from my study suggest that contrasting life histories and demographics may be crucial in competitive interactions between the two species. For example, laminarian development from spore to recruit may take several months (Schiel 1988). In contrast, *C. maschalocarpum* releases comparatively well developed propagules that recruit within 40- 50 days (Schiel 1988). The contrasting life histories of both species means that *C. maschalocarpum* can usually recruit in higher densities than *U. pinnatifida* due to more direct development. In previous studies, *C. maschalocarpum* were found to recruit in densities greater than 5000 m<sup>2</sup>. Although

recruit levels were not that high, in my study *C. maschalocarpum* recruited in greater numbers than *U. pinnatifida*, allowing *C. maschalocarpum* to dominate clearances during the summer when no *U. pinnatifida* plants were present. However, between late autumn and late spring the superior growth rates (about 10 mm per day) of *U. pinnatifida* plants compared with *C. maschalocarpum* plants (100 mm per year) (Schiel 1988) meant that *U. pinnatifida* dominated larger clearances during this period. *Carpophyllum maschalocarpum*, due its perennial life history, was able to regain small amounts of space in the absence of *U. pinnatifida* during the summer. This suggests that the differences in life histories and demographic characteristics between the two species may affect the resistance and resilience of different sized clearances of *C. maschalocarpum* to invasion by *U. pinnatifida*.

The general applicability of native canopy removal experiments must be considered with some caution, as only one site was used due to the lack of suitable areas with *C. maschalocarpum* and *U. pinnatifida* present. Furthermore, Rapaki Bay was the only site where *U. pinnatifida* was absent over extended periods in the summer. At other sites, *U. pinnatifida* may persist all year round (Chapter 2) so competition between the two species may be more intense during the summer.

### Summary

The results of this study show that *U. pinnatifida* has the ability to recruit immediately following a canopy disturbance. *U. pinnatifida* has both an opportunistic life history and demographic traits such as fast growth to reproductive maturity, high reproductive output and extended recruitment periods that possibly increase its chances of successful recruitment. The opportunistic ability of *U. pinnatifida* may be due to either a continual supply of propagules (see Chapter 2) or the presence of a "seed bank" which may allow recruitment during favourable periods (i.e. increased light levels) (Hoffman and Santelices 1991). Although *U. pinnatifida* was able to establish in large areas (25 x 25 cm and 50 x 50 cm) of a disturbed *C. maschalocarpum* stand, its ability to persist for periods longer than 12 months may require continual disturbance. The aim of future studies should examine the ability of *U. pinnatifida* to persist in areas dominated by native algal stands that are subjected



to continual disturbance. Furthermore, if at all possible this should be done at multiple sites.

## **Chapter 5**

# **Early Post-Settlement Survival and Growth**

## 5.1 Introduction

The successful establishment of algae within habitats that experience fluctuating resources is largely due to the ability of species to adapt and evolve different life history strategies (Santelices 1990b). Broad dispersal of propagules can enhance establishment when limiting resources (light, nutrients and space) vary spatially (Dayton 1973, Fernández *et al.* 1990; Reed *et al.* 1997). Moreover, some algae may have an extended reproductive period in order to “hedge” against unfavourable recruitment periods (Hruby and Norton 1979). Marine algae have also evolved responses to exogenous cues, such as photoperiod or temperature that vary predictably with season in order to synchronise propagule production or the emergence of settlers (Lüning 1980; Santelices 1990b; Edwards 2000). Alternatively, to avoid recruitment-limiting periods some algae have developed mechanisms to delay recruitment until favourable recruitment conditions exist (Hoffmann and Santelices 1991; Edwards 2000, Kinlan *et al.* 2003).

Delayed recruitment has been inferred in many laminarian species. For annuals, such as *Postelsia palmaeformis*, in which propagule production is seasonal, there is often an interval of several months between zoospore production and macrosporophyte recruitment. Furthermore, the absence of plants for several months over winter suggests that microscopic stages may persist in the absence of adult populations (Blanchette 1996). The absence of plants may be due to the long development times of newly-settled propagules or microscopic stages remaining dormant for short periods.

In laminarians, the presence of the dormant or slow growing life history stage may provide the ability to delay recruitment during recruitment-limiting periods (Klinger 1993). In most kelps “recruitment windows” are often episodic and they may rely on dormant or slow growing early post-settlement stages to recruit successfully. For example, in *Macrocystis pyrifera*, outplanted gametophytes resulted in successful recruitment of *M. pyrifera* sporophytes when a combination of temperature (below 14°C) and levels of critical irradiance required for gametophyte maturation ( $0.4 \text{ E.m}^{-2}.\text{d}^{-1}$ ) were met (Deysher and Dean 1986). If the “recruitment window” conditions

were not met then gametophytes did not mature (presumably, they lay dormant or grew vegetatively) (Deysher and Dean 1986).

Most studies on gametophytes have been laboratory based due to the inherent difficulties in working with the microscopic stages in the field. Laboratory based studies have shown that under certain light, nutrient and temperature regimes gametophytes could survive and grow (slowly) for extended periods (Kain 1964; Anderson and North 1969; Lüning and Neushul 1978; Lüning 1980; Bolton and Levitt 1985; tom Dieck 1993). More recently, a study on the giant kelp *Macrocystis pyrifera*, provided evidence to suggest that embryonic sporophytes were the life history stage undergoing delayed development (Kinlan *et al.* 2003). Recruitment of embryonic sporophytes was delayed by 1 month when light and nutrient conditions were manipulated to mimic those found under a *M. pyrifera* canopy.

Although there is evidence that both gametophyte and embryonic sporophytes can grow slowly in resource-limited conditions, the persistence of macroalgal “seed banks” within the environment is likely to be short in comparison with terrestrial “seed banks” (Hoffmann and Santelices 1991). The short survival of early post-settlement stages within the “seed bank” is likely to be caused by high levels of mortality experienced in these early stages (Hoffmann and Santelices 1991; Vadas *et al.* 1992). Significant losses of early post-settlement stages may be due to grazing invertebrates (Dayton 1985; Reed *et al.* 1988; Vadas *et al.* 1992). Additional losses may occur through burial and abrasion by sediments (DeVinny and Volse 1978; Dayton 1985; Deysher and Dean 1986; Airoidi 2003). Moreover, extended periods of suboptimal conditions such as low light caused by canopy shading can not only retard growth but also kill early post-settlement stages (Parke 1948; Chapman 1984a). Alternatively, settlement of propagules may occur outside optimal habitats, inhibiting the further development of early post-settlement stages.

The sources of mortality associated with delayed recruitment may affect *U. pinnatifida*. Previous experiments have shown that this species may undergo a period of delayed recruitment when suppressed by canopies (Chapter 4). Lengthy periods spent underneath canopies may harm the survival of early post-settlement

stages. Additional mortality of the early post-settlement stages of *U. pinnatifida* may be caused by macroinvertebrate grazers. In areas where *U. pinnatifida* occurs, large numbers of macroinvertebrate grazers coexist (Chapter 3). These factors may affect the ability of *U. pinnatifida* to delay recruitment.

The ability of kelps to delay recruitment has particular relevance to *U. pinnatifida* because plants at some sites are absent for extended periods over the summer. *Undaria pinnatifida* clearly has the ability to survive as microscopic stages during the summer, as dispersal from other sources is unlikely for a number of reasons. First, the absence of intertidal populations coincides with absence of subtidal populations. Second, large-scale natural dispersal of *U. pinnatifida* has not been shown to occur (Chapter 2) (Forrest *et al.* 2000).

This chapter examines the survival and growth of embryonic sporophytes of *U. pinnatifida* in the field. Gametophytes were not used in this study due to the inherent difficulties in working with such small stages. Macroinvertebrate grazing was examined to determine if grazers were a major cause of mortality of early post-settlement stages. Hypotheses testing the effects of shading on survival and growth were examined to determine the ability of embryonic sporophytes to persist in resource-limiting conditions (low light levels). Further experiments testing hypotheses relating to seasonal growth of embryonic sporophytes were done. Comparisons of development times of spores to visible recruits and embryonic sporophytes to recruits were done to determine if microscopic stages lay dormant or grew slowly during unfavourable recruitment periods.

## 5.2 Methods

Chapter 3 showed that *U. pinnatifida* was a poor coloniser of primary space but a good coloniser of coralline turfs. It was hypothesised that large grazing invertebrates would prevent the colonisation of primary space by grazing the microscopic stages of *U. pinnatifida*. In contrast, the complex form of coralline turfs would inhibit grazing and allow the microscopic stages to develop. An experiment was set up to test the effects of grazers on the survivorship of microscopic stages of *U. pinnatifida* on

primary substratum during the late winter and summer of 2002 at Rapaki Bay and Diamond Harbour.

Chapter 4 showed that removal of the mature *U. pinnatifida* canopy resulted in almost immediate recruitment of *U. pinnatifida*. It was also noted that recruits typically appeared between or near the holdfasts of removed plants. It was hypothesised that the mature adult plants shade many of the microscopic sporophytes and prevent them from growing. It was also hypothesised that survival of the embryonic sporophytes would be greater outside the influence of mature plants. An experiment to test these hypotheses was done at Diamond Harbour during November 2002.

Previous experiments (Chapter 4) showed that removal of a mature *Carpophyllum maschalocarpum* canopy resulted in almost immediate recruitment of *U. pinnatifida*. It was hypothesised that the microscopic sporophytes of *U. pinnatifida* can remain dormant or grow slowly under the canopy of *C. maschalocarpum*. Furthermore, it was hypothesised that the presence of the coralline turfs and the presence of a canopy would slow growth but not affect survivorship. Conversely, it was hypothesised that the absence of coralline turfs would result in slow growth and high mortality due to the scouring nature of the *C. maschalocarpum* fronds. An experiment to test these hypotheses was initiated at Rapaki Bay during October 2002 and repeated again in December 2002.

### *Culturing methods*

Seawater for culturing was collected from the sea, filtered through a 1  $\mu\text{m}$  filter and sterilised through a UV filter. The water was kept in 50 L sealed black plastic containers for two weeks at 14° C to kill any remaining phytoplankton in the water.

The culturing procedure was adapted from methods employed in the mariculture of *Undaria pinnatifida* in China (Dr Michelle Mei *pers. comm.*). Mature sporophylls were obtained from the Diamond Harbour site, cleaned of sediment and epiphytes, transported back to the laboratory wrapped in wet tissue paper and left to desiccate

for two hours in a cool dark area. Once sufficiently desiccated (samples of tissue were examined for spore release) the sporophylls were placed in a 20 L bucket of sterilised seawater and agitated to induce spore release. Once spores had been released (the water became brown) the solution was filtered through a 50 µm sieve to remove sporophyll fragments and amphipods. The stock solution was then diluted to  $1 \times 10^4$  spores per ml.

Zoospores from the stock solution were settled onto the experimental substratum, which consisted of 120 mm long pieces of pre-soaked mariculture string (2 mm diameter). Settlement took place in plastic trays filled with sterilised water. Each piece of string had two knots tied at each end, which allowed 25 mm long (6.5 mm diameter) nylon Ramset™ anchors to be attached at the beginning of each experiment. The knots also allowed the strings to be removed easily without causing damage to the microscopic plants. The presence of the knots meant that the distance between both anchors was only 75 mm. The spores were left to settle for approximately five hours and then the cultures were placed into fresh trays of sterilised water. Glass microscope slides were also placed within the cultures to provide a means of examining developing plants over time. The cultures were grown in a temperature-controlled room at 14 °C with a 12:12 L:D cycle. The water was changed every two days and nutrient broth (see Appendix II for recipe) was added at a rate of 10 ml to every 1L with new water. Diatoms and bacteria were controlled with 2.5 mg. L<sup>-1</sup> of germanium oxide.

#### *Estimation of numbers*

Once sporophytes had begun to appear (between 26-35 days) each piece of culture string was removed from the solution and the sporophytes counted under a binocular microscope (Leica) at 100x magnification. The vast numbers of sporophytes (typically >8000) per string necessitated sub-sampling when counting. Ten random 1 mm<sup>2</sup> quadrats were counted on each piece of string. The length of ten randomly chosen sporophytes were also measured from each string. Because of the relatively uniform covering of sporophytes much of the string surface appeared brown. Any pieces of string that appeared patchy were discarded thus reducing the amount of variation between strings. The estimates obtained were then multiplied by half the

surface area of the available string, as plants on the underside and lower sides of the string would be unlikely to survive when placed on the ground.

### *Transportation*

All culture strings were transported in thermally insulated containers between the laboratory and the field. The strings were placed on wire racks during transportation to stop them rubbing against each other and dislodging sporophytes. This method proved effective in preventing any significant losses during transportation. Controls were used during the setting up and counting of strings to determine if losses occurred as a result of handling and transportation. No losses were recorded during the experiments.

### *Attachment to substrate*

All strings were attached by nailing the two previously attached nylon Ramset™ bolts into the substrata. Strings were placed within the coralline turfs. This method proved effective in holding the strings in place and also allowing the strings to be removed for counting. When removing the strings for counting, tweezers were used and the utmost care was taken not to touch the area between the anchors.

### *Counts*

Initially the number of sporophytes on each string was estimated using 10 random counts of 1 mm<sup>2</sup>, but as plants became bigger they were monitored *in situ* using a magnifying glass (20x). Strings that were counted in the laboratory were returned to the shore on the following tide.

#### **5.2.1 Effects of grazing**

Prior to the experiment, a pilot study was done in the laboratory to determine if grazers could graze the surface of the string. Five *Turbo smaragdus* (the major grazer at the study sites) were starved for three days and then placed in a container with two strings (50 mm in length) coated in *U. pinnatifida* for 8 hours. This was repeated three times with different groups of snails. The strings were grazed heavily (>90% mortality).



The field experiment was done during August 2002 and repeated in November 2002 within the low zone at both sites. The experimental design included replicated ( $n=5$ ) treatments (each of open, caged and cage control) within areas of coralline turfs and areas removed of coralline turfs. Removal treatments were cleared by scraping away the coralline turfs with a masonry hammer. Cages measured 120 x 70 mm with 50 mm high sides and were made from stainless steel mesh (12 holes per  $\text{cm}^2$ ). Each cage had a 20 mm overhanging lip and nylon mesh (15 mm wide) to prevent grazers (mainly *T. smaragdus*) from climbing over the sides and entering. Cage controls had the same dimensions but had 40 mm gaps on the ends and 80 mm gaps along the sides. Open areas had no cage. Treatments were randomly assigned within each of the substratum treatments. Single cultured strings with embryonic sporophytes were then randomly assigned to the five replicates of each treatment and attached using the methods discussed in section 4.2.1. Embryonic sporophytes on strings were counted initially at 21 days and approximately 1 month later using the methods stated in section 4.2.1. Data from grazing experiments were analysed as three-way ANOVA (Statistica 6.0 <sup>TM</sup>), using site, substratum and cage as independent factors (all fixed factors) and the proportion of embryonic sporophytes surviving of the original number as the response variable. Prior to analysis, data were tested for homogeneity of variances using Cochran's test. Appropriate transformations were done as required.

### 5.2.2 Intra-specific canopy effects

The experimental design to test for the effects of *U. pinnatifida* plants on the survival of embryonic sporophytes consisted of two treatments: away from the *U. pinnatifida* plant (outside) and under the *U. pinnatifida* plant (under) ( $n=10$ ) placed within the low intertidal. For the "under" treatment, strings were placed in coralline turfs under the sporophyll and between the rhizoids of the holdfast. Only healthy mature plants were used for the experiment. For the "outside" treatment, strings were placed next to areas removed of adult plants but within the coralline turfs. Sporophytes on strings were counted at 21 days and again at 42 days. The length of 100 randomly chosen sporophytes were measured. The experiment was terminated after 42 days as most of the mature plants had either senesced or had been removed by members of the

public. Data were analysed using one-way ANOVA (Statistica 6.0™) with outside/under canopy treatment as the fixed factor and the proportion of embryonic sporophytes remaining as the variable. Prior to analysis, data were tested for homogeneity of variances using Cochran's test. Appropriate transformations were done as required.

### **5.2.3. Inter-specific canopy effects**

The experimental design consisted of two factors: *Carpophyllum maschalocarpum* canopy (outside and under), coralline turf (presence and absence) (n=10). Strings were placed in treatments covering all combinations of canopy and turf removal. Strings were counted when the tides and weather permitted. The lengths of 100 randomly chosen sporophytes were measured. The experiment initiated during December was terminated after 21 days when large areas of canopy were removed (unknown cause), exposing a number of canopy treatments. Data were analysed using two-way ANOVA (Statistica 6.0™) with canopy and turf as fixed factors and the proportion of embryonic sporophytes remaining as the variable. Prior to analysis, data were tested for homogeneity of variances using Cochran's test. Appropriate transformations were done as required.

### **5.2.4 Embryonic sporophyte growth**

#### *Winter-Spring growth*

In Chapter 2 small numbers of mature sporophytes were found to be releasing spores during July and August (winter). It was hypothesised that the early autumn recruits, which produced the first mature plants in late winter, could be responsible for recruitment episodes observed in spring/early summer at the study sites. To determine if this was the case, growth data from the August grazing experiment (Section 4.2.1) were used. The length of plants from the treatments in coralline turfs was measured at both sites over a period of 89 days. Recruitment of plants <50 mm was assessed, using the methods from Chapter 2 (Section 2.2.1).

### Summer growth

At Rapaki Bay, no sporophytes were seen over the summer of 2000- 2001 and 2001- 2002 (Chapter 2). There was intense recruitment in the following autumn. Because no plants could be found intertidally or subtidally during summer, it was assumed that there must have been a microscopic stage that lay dormant. It was hypothesised that gametophytes or embryonic sporophytes lay dormant over the summer and the onset of autumn brought on rapid development of them. An experiment to test this was done at Rapaki Bay during summer 2002- 2003. The experimental design consisted of two treatments, using spores and microscopic sporophytes. *U. pinnatifida* was cultured in the laboratory to the sporophyte stage as per the methods in Section 4.2.1 during November 2002. Strings (n=30) were placed in the field within the coralline turfs at the extreme low tide mark. On the same day that the sporophytes were placed out, pieces of string (n=56) were seeded with spore inoculum ( $\sim 1 \times 10^4$  per ml) and placed within coralline turfs. This meant that at the initiation of the experiment (late November) there were embryonic sporophytes (lab cultured) and newly-settled spores (field cultured) placed in the field. Initially, ten randomly chosen strings were collected each month, and embryonic sporophytes counted at the lab using the methods described above. The length of 30 randomly chosen sporophytes was measured on each string. By February 2003 only 16 lab-cultured and 11 field-cultured strings were available as the others had become smothered by sediment or ephemeral algae. Closer inspection of the smothered strings revealed no sporophytes. Before the strings were discarded they were kept in aquaria and cultured as though they had *U. pinnatifida* spores present. This ensured that if there were any spores or gametophytes present they would have developed. No sporophytes developed on the strings.

## 5.3 Results

### 5.3.1 Effects of grazing

The presence of coralline turf had a significant positive effect on the survival of sporophytes for both sampling dates during spring and summer (Figs. 5.1; 5.2, Table 5.1; 5.2). However, grazing had no effect on survival for both spring and summer

experiments on either sampling date (Table 5.1; 5.2). During summer, recruit survival was higher at Diamond Harbour than at Rapaki Bay by day 21 within the coralline turf treatments but the differences were not significant (Fig. 5.2, Table 5.2). By day 58, no plants had survived in the coralline turf removal treatments (Fig 5.2). Analysis was done with the remaining coralline treatments. No significant differences were found between sites or cage treatment (Table 5.2).

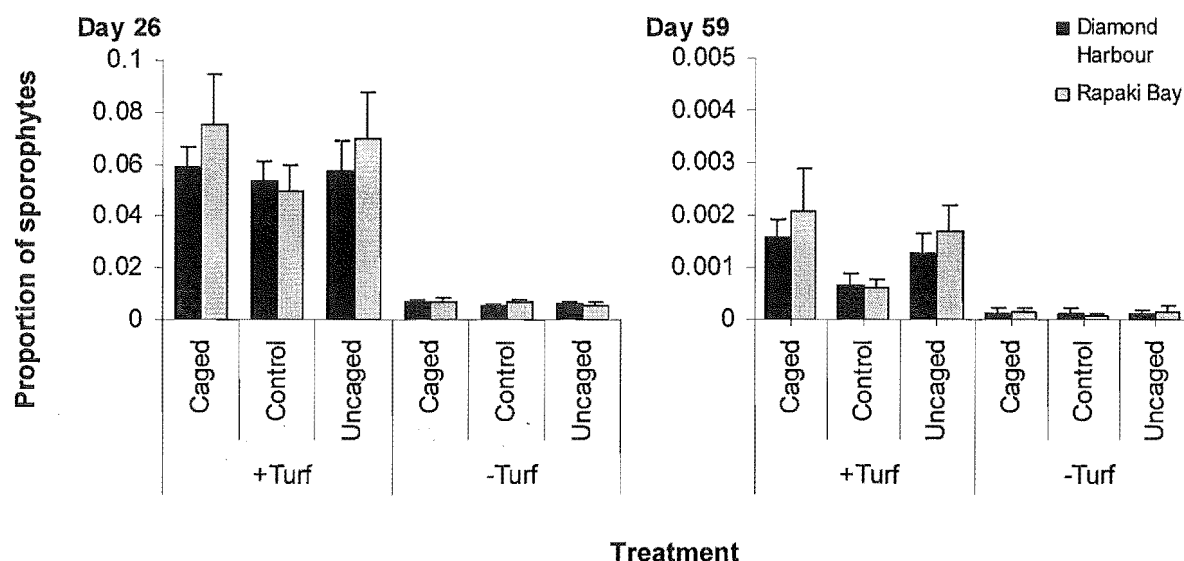


Figure 5.1: Mean proportion (+1 S.E.) of embryonic *U. pinnatifida* sporophytes surviving after 26 and 59 days in different treatments at Rapaki Bay and Diamond Harbour during the spring of 2002 +Turf = coralline turfs.

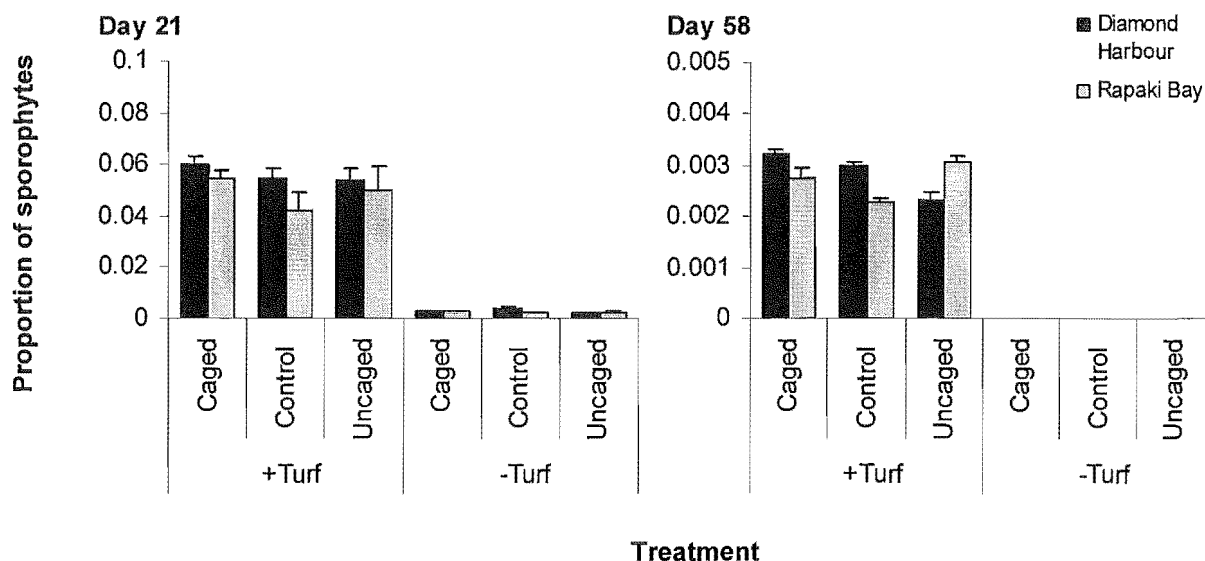


Figure 5.2: Mean proportion (+1 S.E.) of embryonic *U. pinnatifida* sporophytes surviving after 21 and 56 days in different treatments at Rapaki Bay and Diamond Harbour during the summer of 2002 +Turf = coralline turfs.

Table 5.1: Results of three-way ANOVA's on survival of embryonic *U. pinnatifida* sporophytes after 26 days and 59 days during spring and 21 days during summer 2002. Factors are site (Diamond Harbour, Rapaki Bay), substratum (presence or absence of coralline turf), cage (cage, no cage and cage control). \*\*  $p < 0.01$ . Data were square root, arc sine transformed. Cochran's test was not significant.

Effect	df	Spring				Summer	
		Day 26		Day 59		Day 21	
		MS	F	MS	F	MS	F
Site	1	0.00072	0.37	0.00006	0.45	0.00173	3.06
Substrata	1	0.40747	<b>209.11**</b>	0.01025	<b>76.33**</b>	0.47390	<b>837.20**</b>
Cage	2	0.00100	0.76	0.00041	3.04	0.00076	1.35
Site x Substrata	1	0.00200	0.11	0.00002	0.16	0.00091	1.60
Site x Cage	2	0.00011	0.06	0.00002	0.12	0.00055	0.97
Substrata x Cage	2	0.00121	0.62	0.00032	2.39	0.00059	1.04
Site x Substrata x Cage	2	0.00100	0.51	0.00001	0.08	0.00004	0.08
Error	48	0.00020		0.00013		0.00056	

Table 5.2: Results of two-way ANOVA on survival of embryonic *U. pinnatifida* sporophytes after 56 days with coralline turf treatments at Diamond Harbour and Rapaki Bay during the summer of 2002. Data were square root, arc sine transformed. Cochran's test was not significant.

Effect	df	MS	F	p
Site	1	0.000007	0.187	0.670
Cage	2	0.000003	0.072	0.931
Site x Cage	2	0.000043	1.138	0.337
Error	24	0.000038		

### 5.3.2 Intra-specific canopy effects

Mortality was extremely high in the first 22 days for both the treatment and control strings, with sporophyte numbers declining from ~11000 per string to ~300 per string. At 47 days the mortality rate slowed with ~150 plants remaining per string (Fig. 5.3). There was no significant treatment effect of cover on survivorship of embryonic sporophytes under adult *U. pinnatifida* plants at either 22 days ( $F_{(1,18)}=0.16$ ,  $p=0.89$ ) or at 47 days ( $F_{(1,18)}=1.38$ ,  $p=0.25$ ). However, there were significant differences observed in the mean length of plants at both sampling times (Fig. 5.4). After 22 days, plants outside the adult canopy were  $0.4 \text{ mm} \pm 0.007$

whereas those under the adult plants were  $0.1 \text{ mm} \pm 0.007$  ( $F_{(1,198)}=1087$ ,  $p<0.001$ ). This pattern was also observed at 47 days with plants outside the canopy larger ( $0.8 \text{ mm} \pm 0.02$ ) than those under the canopy ( $0.4 \text{ mm} \pm 0.007$ ) ( $F_{(1,198)}=841.21$ ,  $p<0.001$ ).

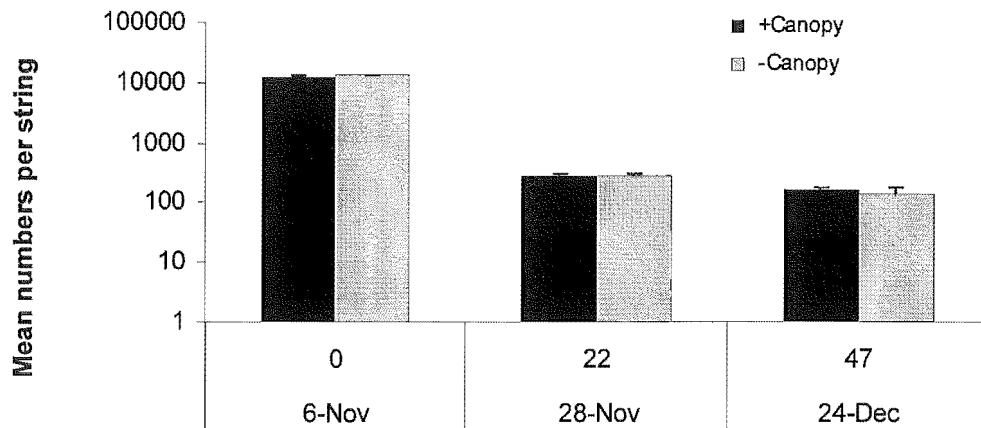


Figure 5.3: Means number ( $\pm 1$  S.E.) of embryonic sporophytes of *U. pinnatifida* at days 0, 22 and 47 outside and under a *U. pinnatifida* canopy at Diamond Harbour.

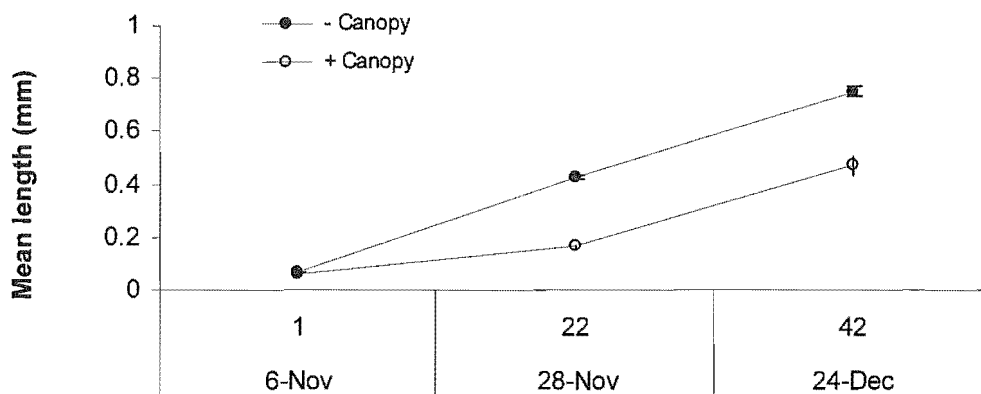


Figure 5.4: Mean length ( $\pm 1$  S.E.) of embryonic sporophytes of *U. pinnatifida* at days 1, 22 and 47 outside and under an *U. pinnatifida* canopy at Diamond Harbour.

### 5.3.3 Inter-specific canopy effects

Embryonic sporophytes of *U. pinnatifida* had highest survival within the coralline turfs both under and outside the *Carpophyllum maschalocarpum* canopy at 24 and 51 days (Fig. 5.5) (Table 5.3). Although there was a significant substrata effect and non-

significant canopy effect there was a significant interaction between canopy and turf treatments for both dates (Table 5.3). This can be attributed to the high rates of survival of plants on the bare substrata under the canopy (Fig. 5.5). Similar survival rate were observed for plants that were found under the canopy during both sampling periods (Fig. 5.5). In contrast, plants that were in the open experienced lower survival at day 51 (Fig. 5.5).

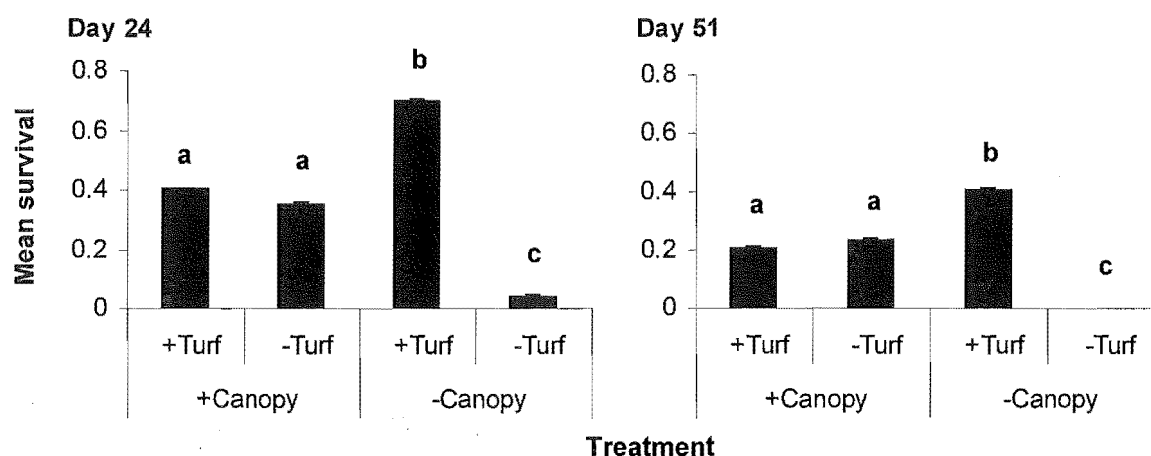


Figure 5.5: Mean proportion (+1 S.E.) of embryonic *U. pinnatifida* sporophytes surviving under the canopy of *C. maschalocarpum* in the presence and absence of the coralline turfs at Rapaki Bay during spring 2002. Survival after 24 days, and 51 days. (a,b,c indicate results of Tukey's HSD test; sites with the same letter were not significantly different at  $p < 0.05$ ).

Table 5.3: Results of two-way ANOVA on the effects of the presence and absence of the coralline turfs and the canopy of *C. maschalocarpum* on the survival of embryonic sporophytes of *U. pinnatifida* after 24 days and 51 days at Rapaki Bay during spring 2002. Data were square root, arc sine transformed. Cochran's test was not significant.

Effect	df	Day 24			Day 51	
		MS	F		MS	F
Substrata	1	0.012494	36.85**		0.00366	28.51**
Canopy	1	0.000004	0.012		0.00002	0.21
Substrata x Canopy	1	0.009035	26.65**		0.00465	36.19**
Error	36	0.000339			0.00001	

The largest plants were found in the +turf -canopy treatment after 51 days (Fig. 5.6). At day 24 there were significant effects of canopy and substrate on the length of plants (Table 5.4). More importantly, there was a significant interaction of canopy and substrate on the mean length of plants. The *C. maschalocarpum* canopy

suppressed growth of sporophytes but, outside the canopy, the turfs enhanced growth

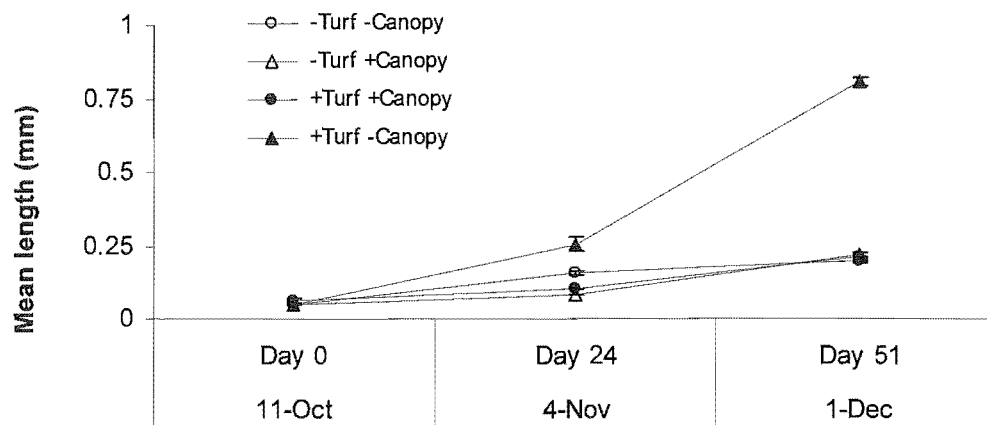


Figure 5.6: Mean length ( $\pm 1$  s.e.) of embryonic *U. pinnatifida* sporophytes in different experimental treatments within the *C. maschalocarpum* canopy at Rapaki Bay over 51 days.

Table 5.4: Results of two-way ANOVA on the effects of the presence of coralline turfs and the canopy of *C. maschalocarpum* on the growth of embryonic sporophytes of *U. pinnatifida* after 24 days and 51 days at Rapaki Bay during spring 2002. Data were log-transformed. Cochran's test was not significant.

Effect	df	Day 24			Day 51	
		MS	F		MS	F
Substrata	1	11.246	<b>101.3**</b>		1.58954	<b>454.854**</b>
Canopy	1	42.439	<b>382.27**</b>		1.5279	<b>437.213**</b>
Substrata x Canopy	1	1.308	<b>11.78**</b>		1.62633	<b>465.38**</b>
Error	396	0.111			0.00349	

Very few sporophytes survived to day 83 (11 and 6 for canopy and –canopy treatments respectively). To analyse the differences in mean length of plants, results were pooled across the turf treatments. Sporophytes were significantly larger outside the canopy ( $1.4 \text{ mm} \pm 0.18$ ) than under the canopy ( $0.45 \text{ mm} \pm 0.07$ ) ( $F_{(1,32)} = 125$ ,  $p < 0.001$ )(Fig. 5.7).

Results of the same experiment repeated during the summer were similar to those done in spring with highest survival occurring within the coralline turfs (Fig 5.7). Although the coralline turfs seemed to have a positive effect on survivorship (Table 5.5) there was no significant effects of shading by the *C. maschalocarpum* canopy



on the survival of plants. Similarly, this can be attributed to the high rates of survival of plants on the bare substrate under the canopy (Fig. 5.7). The most notable difference between the spring and summer experiments was that after 21 days the summer strings became smothered with ephemeral species in all treatments. This resulted in high mortality of sporophytes and the experiment was terminated.

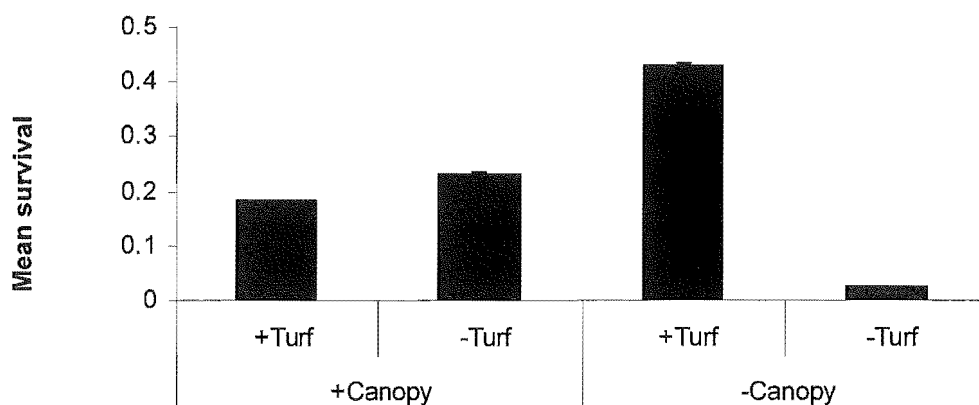


Figure 5.7: Mean proportion (+1 S.E.) of embryonic *U. pinnatifida* sporophytes surviving after 21 days under the canopy of *C. maschalocarpum* in the presence and absence of coralline turfs at Rapaki Bay during summer 2002.

Table 5.5: Results of two-way ANOVA on the effects of the presence and absence of coralline turfs and the canopy of *C. maschalocarpum* on the survival of microscopic sporophytes of *U. pinnatifida* after 21 days at Rapaki Bay during summer 2002. Data were square root, arc sine transformed. Cochran's test was not significant.

Effect	df	MS	F	p
Substrata	1	0.4791	59.07	p<0.01
Canopy	1	0.0187	2.31	0.13
Substrata x Canopy	1	0.0781	92.46	p<0.01
Error	36	0.0081		

### 5.3.4 Embryonic sporophyte growth

#### Natural recruitment

Recruitment of *U. pinnatifida* occurred from August 2002 until November 2002 at both sites (Fig. 5.8). A hiatus occurred over summer (December 2002- February 2003), broken by the appearance of new recruits in March 2003. Recruit abundance

of ~ eight plants per 0.25 m<sup>2</sup> occurred at Diamond Harbour in October 2002 and March 2003. Maximal recruitment at Rapaki Bay occurred during April 2003.

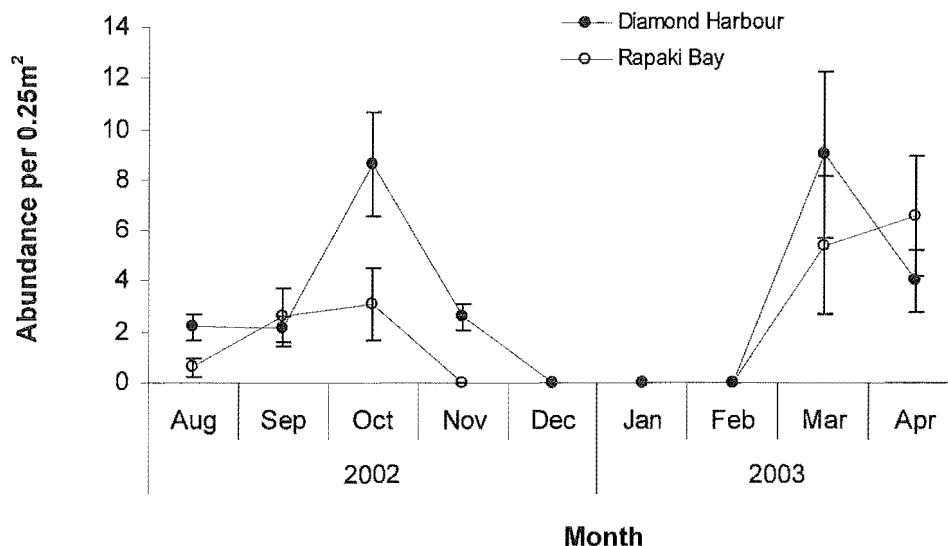


Figure 5.8: Total number of new *U. pinnatifida* recruits (plants <50 mm in length) per 0.25 m<sup>2</sup> ( $\pm 1$  S.E.) at Diamond Harbour and Rapaki Bay between August 2002 and April 2003.

#### Winter-Spring growth

Embryonic sporophytes between Days 1 and 21 grew < 0.5 mm in length (Fig. 5.9). After 21 days plants grew more rapidly and reached 2.3 mm in length by day 66. After 80 days (mid October 2002) plants at Diamond Harbour were ~ 10 mm long while those at Rapaki Bay were only ~8 mm long (Fig. 5.9).

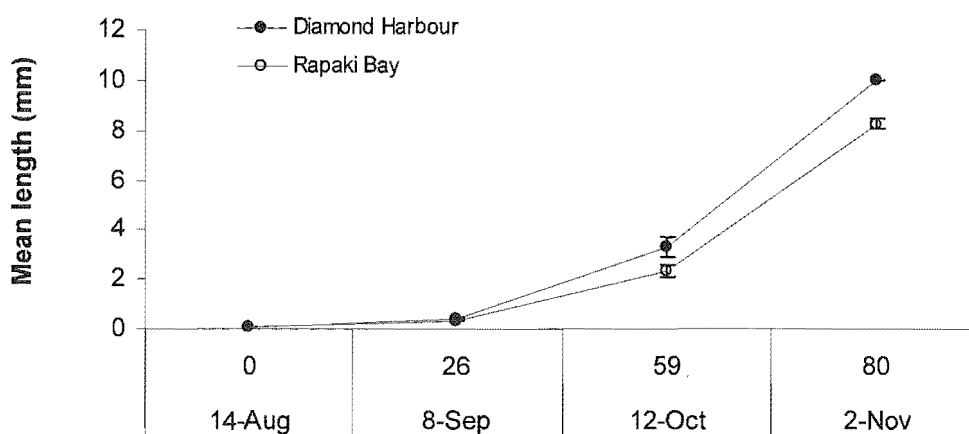


Figure 5.9: Mean length ( $\pm 1$  S.E.) of embryonic *U. pinnatifida* sporophytes (mm) at Diamond Harbour and Rapaki Bay. Data were collected from plants measured as part of the spring grazing experiment.

*Summer growth*

High mortality of plants occurred during the first month of the lab cultured plants being in the field (Fig. 5.10). Initial numbers were approximately 4000 per string at day 0 but this dropped to ~100 per string after 29 days. From December to January, mortality decreased, but by February an increase in mortality meant that low numbers were found. These plants were visible to the naked eye but were no greater than 5 mm in length. In March, recruits of ~16 mm were clearly visible on the string but only in small numbers (Fig. 5.10). From day 84 onwards, greater numbers (~10x) of "field vs lab" embryonic sporophytes were present. In March and April when large natural recruitment was observed, the spore treatments (Field) had ~ 0.005 % survival whereas embryonic sporophyte survival (Lab) was ~ 0.00025 %.

For cultures undertaken in the field, no sporophytes were found until early January (day 58). Strings that became smothered by ephemeral algae were ignored for this analysis. Initial counts of sporophytes were lower than those observed for the lab cultured plants (~4000 vs ~800). By day 84 ~100 plants of 0.3 mm were found. From January to May 2003, the sporophytes grew exponentially in length from ~0.1 mm to ~20 mm.

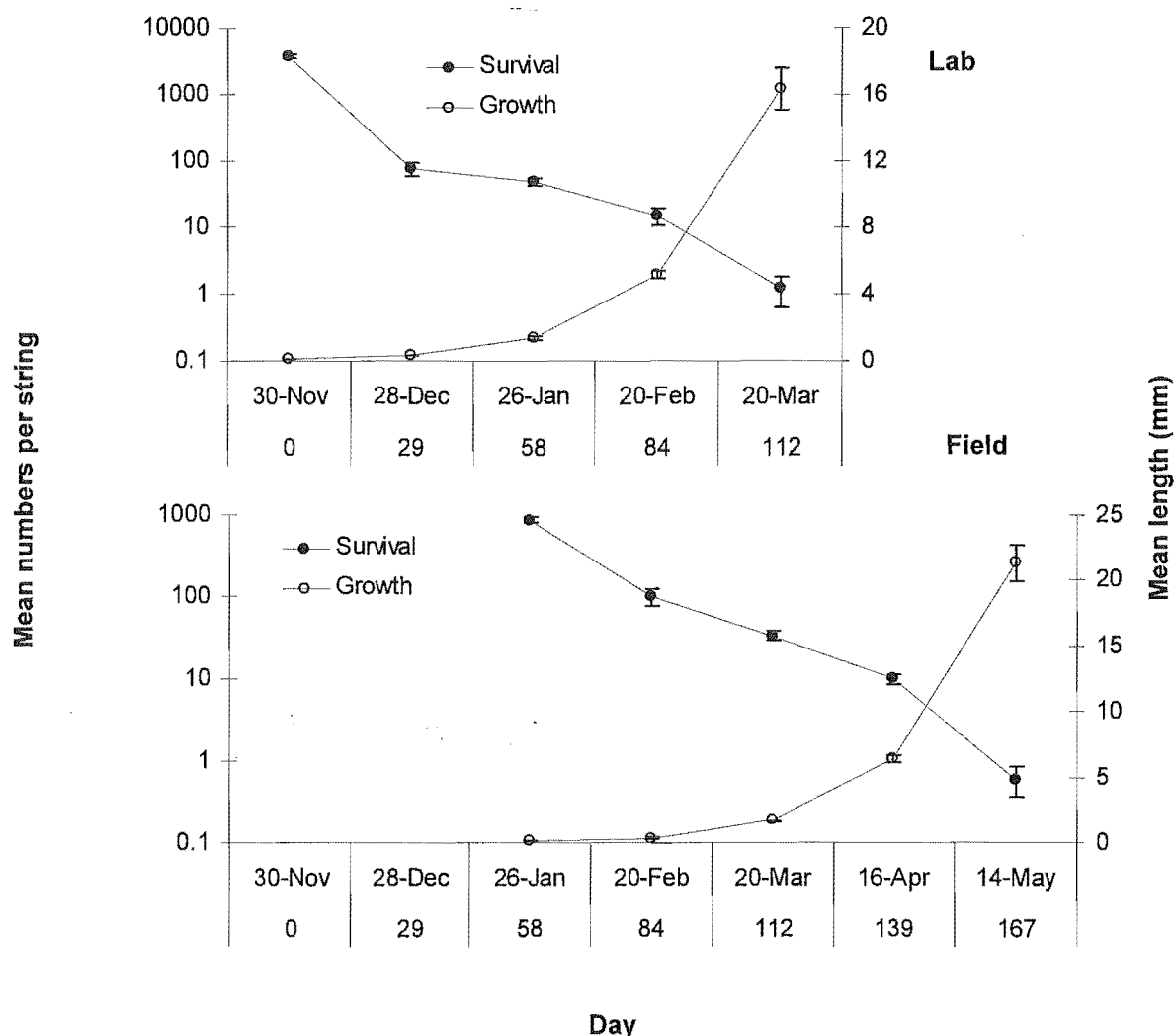


Figure 5.10: Mean growth and survival ( $\pm 1$  S.E.) of embryonic *U. pinnatifida* sporophytes at Rapaki Bay over the summer of 2002-2003. Lab experiments denote embryonic sporophytes that were placed in the field on Day 0 and Field experiments denote spores were placed into the field on Day 0. Note different scales.

## 5.4 Discussion

Survival of *Undaria pinnatifida* embryonic sporophytes for all experiments was lowest during the first three weeks of outplanting with >90% of plants dying. Subsequent mortality throughout the experiments resulted in approximately ~0.00025% of embryonic sporophytes surviving to recruit stage. Although high mortality of early post-settlement stages is typical of most marine algae (Schiel 1985a; Reed 1990a; Vadas *et al.* 1992), the survival rates of *U. pinnatifida* were much higher than previous figures of kelp survival. In species of *Laminaria* an estimated 0.0002 -

0.00001% propagules survive to visible recruits (Chapman 1984a&b). The low survival of early post-settlement stages of laminarians including *U. pinnatifida* can probably be attributed to a number of biological and physical factors such as density-dependence, and desiccation.

Density-dependent mortality of embryonic sporophytes may have occurred, as initial densities of plants on the strings were quite high. Many studies on algae have shown that high initial densities of plants can have negative effects on survival, growth and reproduction (Black 1974; Chapman 1986). However, these studies have concentrated on visible stages and the results may not be applicable to embryonic sporophytes of *U. pinnatifida*. Very few studies have examined the effect of density on survival of early post-settlement stages. Reed *et al.* (1991) found that increased spore settlement density of *Pterygophora californica* resulted in decreased sporophyte production in nutrient limiting conditions. It may be possible that embryonic sporophytes of *U. pinnatifida* experience similar density-dependent effects to that of early post-settlement stages of *P. californica* but this would need to be examined in the future.

Subsequent mortality of embryonic sporophytes after three weeks was probably the result of extremes in environmental conditions and not experimental factors. Grazing by macroinvertebrates seemed to have no effect on the survival of these stages during spring or summer. Instead, plants that were placed within bare substrata perished over a short period. The basaltic rock at Rapaki Bay and Diamond Harbour dried out very quickly during periods of exposure. Desiccation, light and temperature may all have been more intense on these open surfaces (Davison and Pearson 1996) and early post-settlement stages are known to be particularly susceptible to these stresses (Schonbeck and Norton 1978; Lüning 1980; Brawley and Johnson 1991; Vadas *et al.* 1992; tom Dieck 1993). For example, survival of *Pelvetia fastigata* embryos is greatly reduced on bare substrata when exposed at low tide (Brawley and Johnson 1991). It is possible that desiccation prevents *U. pinnatifida* recruitment on bare rock by causing high mortality in the early post-settlement stages. However, the effects of desiccation on the survival of embryonic stages of *U. pinnatifida* are unknown and require further investigation.

The coralline turfs possibly provided embryonic sporophytes relief from desiccation. During periods of exposure, the coralline turfs remained quite moist and this was probably important in enhancing survival rates. Although survival of embryonic sporophytes was higher in the presence of coralline turfs large numbers of sporophytes still perished in those treatments. Turfs not only provide shelter but they harbour large numbers of mesograzers such as amphipods and small snails. These small grazers have been shown to cause substantial mortality in early post settlement stages of some brown algae (Duffy and Hay 2000) and they have resulted in the mortality of embryonic sporophytes in *U. pinnatifida*.

Although the presence of coralline turf facilitated survival of embryonic sporophytes, underneath the *Carpophyllum maschalocarpum* it had no effect on the survival of embryonic sporophytes. In areas devoid of coralline turf, underneath the canopy, embryonic sporophytes survival was similar to areas that had coralline turf. This suggests that the dense *C. maschalocarpum* canopy may shade the embryonic sporophytes of *U. pinnatifida* and shelter them from the harsh environmental conditions. For at least some species, survival is greater for early post-settlement stages in damp areas than those exposed to drier conditions (Brawley and Johnson 1993).

The presence of the *C. maschalocarpum* canopy had no effect on survival of embryonic sporophytes but had a negative effect on growth. At day 51 plants outside the canopy within the coralline turf were three times the size of plants found underneath the canopy. In comparison, the suppressive effect of mature *U. pinnatifida* plants was not as great as *C. maschalocarpum* as the length of embryonic sporophytes away from the mature plants were only twice the size of plants underneath mature plants. Furthermore, the survival of embryonic sporophytes underneath mature *U. pinnatifida* plants was no different to embryonic sporophytes that were away from mature plants.

Differences in growth may be attributed to the availability of "recruitment windows" following a canopy removal. The increased light levels following canopy removal may provide embryonic sporophytes with critical amounts of light required for growth.

Dense subtidal canopies of kelp can reduce light up to 99 % (Reed and Foster 1984) and have been shown to inhibit the recruitment of understory species (Pearse and Hines 1979; Kimura and Foster 1984; Schiel 1985b; Deysher and Dean 1986; Vadas *et al.* 1992; Dayton *et al.* 1992). *Carpophyllum maschalocarpum* forms a dense canopy, which probably reduced light levels and suppressed growth of embryonic sporophytes. Removal of the canopy may provide “recruitment windows” for embryonic sporophytes by providing critical light levels needed for growth. In *Macrocystis pyrifera*, canopy removal resulted in successful recruitment of outplanted gametophytes. The observed “recruitment window” was thought to be a combination of low temperatures (below 14°C) and irradiance levels above the critical levels required for gametophyte maturation ( $0.4 \text{ E.m}^{-2}.\text{d}^{-1}$ ) (Deysher and Dean 1986). The ability of *U. pinnatifida* embryonic sporophytes to grow rapidly following a canopy disturbance suggests that it can make use of “recruitment windows” by the presence of pre-existing embryonic sporophytes underneath the canopy.

The ability of canopies to suppress growth but not negatively affect survival of embryonic sporophytes of *U. pinnatifida* suggests that embryonic sporophytes may be able to delay recruitment, at least for a short time. Delayed recruitment has been suggested as an adaptation to ensure recruitment of algae following unfavourable recruitment periods (Hoffmann and Santelices 1991; Kinlan *et al.* 2003). There is considerable debate about which microscopic stage of kelps have the ability to delay recruitment. Several studies have suggested that the ability of gametophytes to undergo vegetative growth in unfavourable conditions is important in delaying recruitment for kelps. The majority of these studies have been laboratory based and have shown that many aspects of gametophyte biology are synchronised using environmental cues such as photoperiod, spectral quality of light and temperature (Anderson and North 1969; Lüning and Dring 1972; Lüning 1980; Lüning and tom Dieck 1989). In laboratory studies, Edwards (2000) found that the gametophyte was responsible for delayed recruitment in *Desmarestia ligulata* and could survive for at least 15 months. In contrast, Kinlan *et al.* (2003) found that by manipulating the supply of nutrients and light to embryonic sporophytes of *Macrocystis pyrifera* they were able to delay recruitment by one month. The authors suggested that embryonic

sporophytes may be better adapted than the gametophytes at delaying recruitment (Kinlan *et al.* 2003).

The evidence from my study suggests that the embryonic sporophytes of *U. pinnatifida* may be better at delaying recruitment than the gametophytes for a number of reasons. First, successful fertilisation of kelp gametophytes is density-dependent and requires male and female gametophytes to be in close proximity to each other (Reed 1990b; Reed *et al.* 1991). Reed (1990b) found that settlement density of at least 1 spore/mm<sup>2</sup> was necessary for successful recruitment of *M. pyrifera* and *Pterygophora californica*. Second, for delayed recruitment to occur the gametophytes would need to persist in high densities over long periods. It has been shown in laboratory studies that gametophytes were only able to maintain the correct densities for eight weeks (Kinlan *et al.* 2003). In field studies, the survival of gametophytes may possibly be lower due to other factors such as grazing, sedimentation, and competitive interactions (Vadas *et al.* 1992). Third, the spores and gametophytes would be more susceptible to benthic boundary conditions such as water turbulence than embryonic sporophytes (Vogel 1984). However, it is possible that embryonic sporophytes may be subjected to additional sources of mortality such as mesograzers, sedimentation and smothering by ephemeral species.

The absence of plants during the summer months at Rapaki Bay and the sudden appearance of recruits in the autumn is probably the result of embryonic sporophytes growing slowly over summer and not the presence of dormant stages which subsequently grow rapidly during late summer to recruit in autumn. Spore treatments that were placed in the field resulted in visible recruits appearing approximately 40 days later than the embryonic sporophyte treatments that were placed in the field at the same time. This suggests that the gametophyte is unlikely to undergo a period of dormancy or vegetative growth as combined development times of spores and gametophyte maturation are similar to the time differences observed between spore treatments and embryonic sporophyte treatments (spores ~1-3 days, gametophytes 10-24 days Akiyama (1965), 23-37 days (Stuart 1997).



Embryonic sporophytes of *U. pinnatifida* took approximately one month longer to appear in the summer than in the winter (4 vs 3 months). The slight differences in growth rates may be attributed to higher sublethal temperatures experienced during the summer, which may have slowed growth. Alternatively, slower growth of embryonic sporophytes during the summer may have been due to lower nutrient levels that can occur within coastal embayments within the South Island during summer (Gibbs *et al.* 2002). Embryonic sporophytes of *M. pyrifera* are particularly susceptible to nutrient fluctuations with growth reduced during periods of low nutrient availability (Kinlan *et al.* 2003).

During winter, *U. pinnatifida* embryonic sporophytes grew exponentially, becoming visible during mid spring. The appearance of recruits coincided with peaks in recruitment, suggesting that propagules released during winter by the previous autumn cohort may be responsible for cohorts that appear in spring. This would suggest that *U. pinnatifida* is not a strict annual but possibly a bi-annual. However, the fact that embryonic sporophytes were initially cultured in the laboratory for approximately one month suggests the need for some caution when drawing this conclusion, as development times of spores and gametophytes may be extended during the cooler winter months (Stuart 1997).

### Summary

Reproductive responses to episodic and stochastic events are important in the population structure and persistence of many algal species. For *U. pinnatifida*, the mechanism that enables this species to recruit rapidly when favourable conditions occur appears to be the ability of the embryonic sporophytes to persist in unfavourable conditions. Grazing by macroinvertebrates had no effect on survival of embryonic sporophytes at Lyttelton Harbour. Shading by canopy had no negative effect on the survival of embryonic sporophytes and in the case of *C. maschalocarpum* assisted the survival of embryonic sporophytes in the absence of coralline turfs. The ability to avoid these causes of mortality through either facilitation by coralline turf or reducing growth during unfavourable conditions may provide the invasive mechanism for *U. pinnatifida* to establish in intertidal areas of New Zealand.

Major causes of mortality in this species were not determined in this study but further work should examine the effects of desiccation and grazing by mesograzers.

## **Chapter 6**

### **General Discussion**

## 6.1 General Discussion

This thesis examined the mechanisms involved in the establishment and persistence of populations of the Asian kelp *Undaria pinnatifida* in southern New Zealand. It is well known as an invasive species and has spread from its place of origin in Japan, Korea and China to many temperate areas of the world. A major feature of invasiveness is the localised expansion of populations once a species arrives in a new area. It seems clear that far more species arrive in ballast water of ships and on ship hulls than become firmly established in new areas (Carlton and Geller 1993; Carlton 1996; Ruiz *et al.* 1997). Therefore, the particular characteristics of species that enable them to become established, thrive and spread are of considerable importance. Such species must persist in an environment often laden with native species with which they may interact strongly as their populations become established. The ability of a species to spread is clearly related to the particular characteristics of its morphology and physiology, demographic patterns, life history and dispersal potential.

Here I discuss these characteristics as they relate to *U. pinnatifida* and its interactions with other species in southern New Zealand, particularly with the algal turfs and fucalean species that are common in the intertidal-subtidal fringe.

### *Demography*

*U. pinnatifida* is an annual species that can produce distinct cohorts throughout autumn - late spring in southern New Zealand. Populations can contain visible plants during the warmer months of summer, but their numbers are highly variable among sites with some having populations with no visible plants present during the summer. In their initial assessment of this species in Wellington Harbour, Hay and Villouta (1993) observed that *U. pinnatifida* seemed to have a much more extensive season of growth, reproduction and recruitment in New Zealand than in its native Asian habitats. Subsequent studies at other points of introduction in New Zealand revealed similar demographic patterns with multiple cohorts present at the same time and persistence of plants throughout the summer (Hay and Villouta 1993). They

speculated that the extensive reproductive period and presence of multiple cohorts was a major reason why *U. pinnatifida* might spread rapidly in New Zealand.

In the 17 years since Hay and Luckens' (1987) study, it seems fairly certain that the spread of *U. pinnatifida* between coastal sites has been due mostly, or entirely, to vectoring by ships and boats. There are no continuous populations along the coast, but rather distinct localised populations, mostly where boating and shipping are common, such as around ports and harbours. These localities have acted as "seed" sites from which localised populations have expanded. In some cases, such as around Moeraki, the expansion along the coastline from the initial point of invasion has been only a few hundred metres over 8 years, but the populations have become very dense during that period (Schiel *unpublished data*). However, regardless of density, expansion has not occurred along the open exposed coast.

The initial conditions for expansion of a population are that plants must mature and produce viable spores. At all the study sites, this occurred within 3-4 months of recruits appearing. Rapid growth to maturity is indicative of many annual kelps. For example, sporophytes of *Alaria nana* appear in spring and are mature throughout the summer (Pfister 1992). For perennial laminarian species, such as *Laminaria saccharina*, maturity is reached after 8-12 months (Parke 1948) whereas for *L. hyperborea* maturity takes approximately 3 years (Kain 1975). Populations of *U. pinnatifida* were able to produce viable spores from mid winter until late summer, a period of about 7 months. *Undaria pinnatifida* is probably able to expand within localised areas because it is an annual species with a very high reproductive output and long recruitment periods.

Establishment of new populations requires the dispersal of propagules. Many kelps are thought to have limited dispersal because fertilisation of propagules can only occur when spores have settled (Reed 1990b). Consequently, spores have to settle in high enough densities for male and female gametophytes to be in close proximity for successful fertilisation to occur. For example, Reed (1990b) showed that spores of *Macrocystis pyrifera* and *Pterygophora californica* needed to settle at densities of 1 per mm<sup>2</sup> for successful gametophyte fertilisation. To increase dispersal potential,

algae may release spores, simultaneously so there is a greater chance of spores settling in high enough densities for fertilisation to occur. Reed *et al.* (1997) showed that reproductive synchrony in *Macrocystis pyrifera* and *Pterygophora californica* was critical for the dispersal of spores over extended distances, and was likely to play a major role in recolonising areas destroyed by disturbances such as storms.

The life history of annual kelps is conducive to reproductive synchrony as most populations reproduce over a discrete period. However, the few studies that have examined spore dispersal in these species have shown that spores are relatively poor dispersers. For example, *P. palmaeformis*, which occupies wave-exposed coasts of the north-east Pacific, exudes spores down its stipe during low tide when exposed to air (Dayton 1973). As a consequence, of avoiding water turbulence during low tide, colonisation of recruits occurs within 3 m of the parent plant (Dayton 1973). Although *U. pinnatifida* shows a great deal of extended reproductive synchrony, with most plants reproducing between spring and late summer, the localised dispersal from parent plants is on the scale of metres. Forrest *et al.* (2000) found that spores released in tidal currents in the Marlborough Sounds of New Zealand were only effective at establishing plants 10 m down-current from the point of release, and I found the majority of spores within 1 m of the parent plant. The poor natural dispersal of *U. pinnatifida* suggests the species will encroach slowly into new areas once it has been introduced and that the establishment of new populations is reliant on other mechanisms such as human mediated vectors.

For annual marine algae, persistence of populations is largely related to their ability to replace themselves readily. In New Zealand *U. pinnatifida* has an extended recruitment period from autumn to late spring. Hay and Villouta (1993) suggested that the continual arrival of recruits for the majority of the year was a mechanism that allowed *U. pinnatifida* to persist in New Zealand. The persistence of *P. palmaeformis* is determined by wave-induced disturbances and by successful anti-competitive interactions with other species that occupy the substratum. For example, new recruits of *P. palmaeformis* resist competitive exclusion by settling on the mussel *Mytilus californianus*. Individuals of *P. palmaeformis* become so large that the

mussels are ripped from the substratum thereby allowing zoospores to settle in newly cleared areas and develop over the summer (Dayton 1973).

Many annual reproducing kelps exhibit opportunistic patterns of colonisation and as a consequence are considered fugitive species. The degree of flexibility in life history characteristics is considered an important component in the success of annual species when establishing and persisting in new environments (Dayton 1973; Pfister 1991; Blanchette 1996). Initial studies done on populations around New Zealand suggested that *U. pinnatifida* had a flexible life-cycle. Populations at Wellington, Timaru and Oamaru exhibited an aseasonal annual cycle with mature and newly recruited plants present together in most months of the year (Hay and Villouta 1993). The populations considered in my study were also aseasonal with overlapping cohorts. However, my study provided evidence that two generations may complete their life histories in one year. Plants that recruited during autumn were reproductive and releasing spores by winter. Field trials showed that the time taken for development of the spores to visible recruits was approximately 4 months. Recruits therefore became visible in spring, a period when increased recruitment was observed. These spring recruits then developed into mature plants over the summer, released spores and further recruits appeared the following autumn. I am unaware of any other annual laminarian that can produce more than one generation in one year.

The life cycle of *U. pinnatifida* within intertidal areas along southern New Zealand is encapsulated in Figure 6.1 but includes two assumptions. First, spore release must occur in winter when seawater temperatures are below the minimal temperature required for sporophylls to release spores (but see Chapter 2). Second, if spores are released, subsequent development of microscopic stages are not inhibited by extrinsic factors such as shading or density-dependent factors that would slow growth of early post-settlement stages.

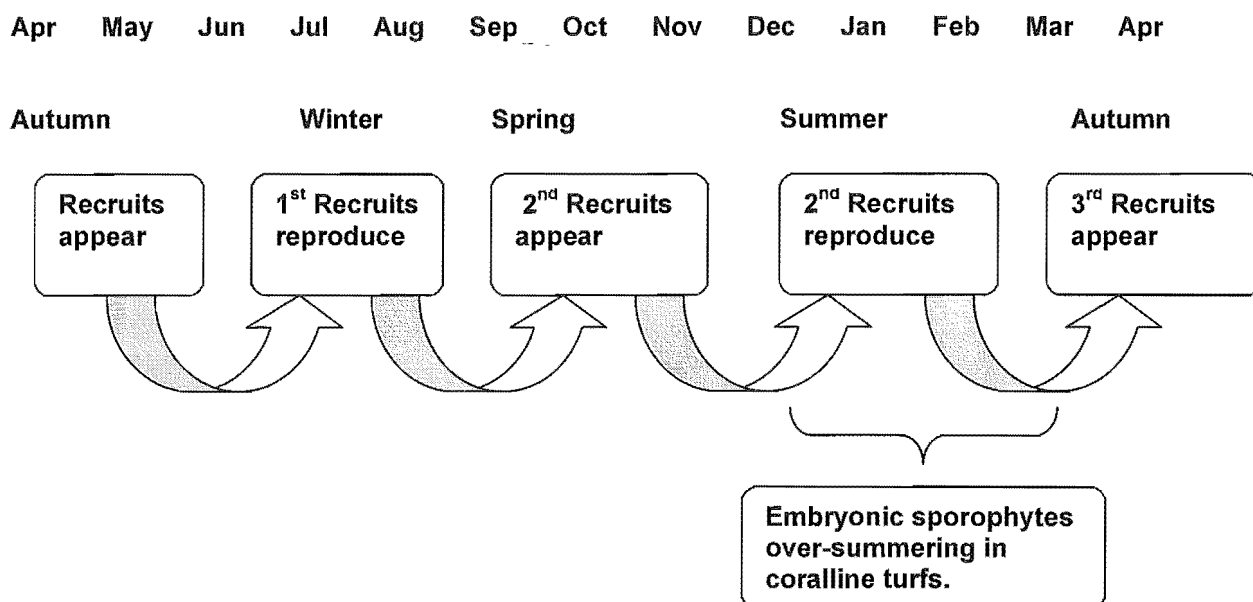


Figure 6.1: Proposed life cycle of *U. pinnatifida* within intertidal habitats along the east coast of the South Island, New Zealand.

### *Persistence of populations*

The successful recruitment of propagules is a major factor in the persistence of algal populations. Persistence can be achieved, either by populations replacing themselves, or by propagules being dispersed to new areas. In an environment where early post-settlement survivorship is low, many species have evolved adaptations to ensure successful recruitment (Chapman 1984a, Schiel 1985a). For example, macroalgae may increase propagule pressure by increasing reproductive output, or by ensuring high survival rates of propagules. In fucaleans well developed propagules are produced due to the direct development of gametes after fertilisation (Dawson 1940). In an extreme example, the invasive fucoid *Sargassum muticum* releases well-developed germlings, which potentially allows a greater chance of survival to recruitment (Fernández *et al.* 1990). In contrast, laminarians increase propagule pressure by producing large numbers of spores (in excess of  $10^7$  per plant), which undergo a lengthy developmental period. For example, *Nereocystis luetkeana*, which forms dense forests along the west coast of the US, can produce  $37 \times 10^{11}$  spores per year (Chapman 1984b). The reproductive potential of *U. pinnatifida* estimated in my study was approximately  $10^8$  -  $10^9$  spores per plant. This is within the range of most laminarian species and suggests that although reproductive output is high, a combination of other factors such as habitat



availability, the persistence of microscopic stages during unfavourable recruitment periods and relatively benign competitive interactions are probably involved in the persistence of this species within the intertidal zone of southern New Zealand.

For many seaweed species persistence of populations may depend, at least partially, on the ability to form a "seed bank" of microscopic stages. The "seed bank" ensures successful recruitment within environments where favourable recruitment periods are unpredictable in time (Hoffmann and Santelices 1991). In laminarians, the "seed bank" is considered to be the gametophyte stage, which can grow vegetatively in complete darkness and then begin reproducing when exposed to light (Kain 1964; Lüning 1980). Kain (1964) showed that when gametophytes of *L. hyperborea* were subjected to 10 days darkness and then placed in high light conditions ( $220 \mu\text{g.cal/cm}^2\text{sec}$ . 12:12 L:D) at 10 °C they became fertile at approximately 21 days after the light treatment. Lüning (1980) found that primary cell gametophytes (recently germinated embryospores) of *L. hyperborea* and *L. saccharina* could be kept in darkness for 5 months and then produce sporophytes after being saturated by light (2000-3000 lux). Alternatively, recent studies have shown that the embryonic sporophyte may be the stage, which provides the "seed bank". Kinlan *et al.* (2003) found that by manipulating the supply of nutrients and light to embryonic sporophytes of *Macrocystis pyrifera* they were able to delay recruitment by 1 month. Although there is evidence that both gametophyte and embryonic sporophytes can grow slowly in resource-limited conditions the persistence of "seed banks" within the marine environment is likely to be short in comparison with terrestrial "seed banks", which can last for years (Hoffmann and Santelices 1991).

Embryonic sporophytes and not gametophytes of *U. pinnatifida* are likely to act as a "seed bank" for several reasons. First, successful fertilisation of kelp gametophytes is density-dependent and requires male and female gametophytes to be in close proximity to each other (Reed 1990b; Reed *et al.* 1991). Persistence of gametophytes for extended periods of time would be unlikely due to high mortality from grazing, sedimentation, and competitive interactions (Vadas *et al.* 1992). For example, Kinlan *et al.* (2003) could only maintain gametophytes in the laboratory at appropriate densities for fertilisation for 8 weeks (Kinlan *et al.* 2003). Instead, results

from my study suggest that the embryonic sporophytes may be better adapted at delaying recruitment during unfavourable conditions (low light or harsh summer conditions).

### *Facilitation*

The persistence of *U. pinnatifida* within intertidal areas along the east coast of the South Island is probably due to the facilitative conditions provided by coralline turfs, which are likely to provide relief for microscopic stages from harsh environmental conditions. Although other studies have shown that subtidal turfing algae can accumulate sediments that are likely to inhibit recruitment of macroalgae (Airoidi *et al.* 1996) the coralline turfs within the intertidal zone at the study sites had very little sediment trapped within them (*pers. obs.*). This was probably due to the continual re-suspension of sediment by incoming waves.

Increased desiccation, light levels and temperature may have resulted in a paucity of recruitment and low survival of embryonic sporophytes within bare substrata at my study sites. Previous studies have shown that early post-settlement stages can be particularly susceptible to these stresses (Schonbeck and Norton 1978; Lüning 1980; Brawley and Johnson 1991; Vadas *et al.* 1992; tom Dieck 1993; Davison and Pearson 1996). For example, survival of *Pelvetia fastigata* embryos that settled on bare substrata was poor due to increased desiccation rates experienced by the embryos (Brawley and Johnson 1991). It is possible that desiccation prevents *U. pinnatifida* recruitment on bare rock by causing high mortality in the early post-settlement stages.

During periods of exposure, I found that coralline turfs remained quite moist, a condition that was probably important in enhancing survival rates. However, turfs not only provide shelter for microscopic stages but they also harbour large numbers of mesograzers such as amphipods and small snails. These small grazers have been shown to cause substantial mortality in early post-settlement and macroscopic stages of some brown algae (Dayton *et al.* 1984; Duffy and Hay 2000; Lotze and Worm 2000; Lotze *et al.* 2002). Mesograzers within coralline turfs may reduce the

survival of early post-settlement stages of *U. pinnatifida* but this requires further investigation.

Grazing by large gastropods such as *Turbo smaragdus* was not a major cause of mortality for embryonic sporophytes of *U. pinnatifida*. However, the results obtained in my study may be site specific as the experiments were done only at the Lyttelton Harbour sites. It is possible that grazers may have an effect on the survival of early post-settlement stages at the Moeraki sites, especially Moeraki Platform due to greater abundances of *T. smaragdus* ( $>50 \text{ m}^{-2}$ ). Although other macroinvertebrate grazers including *Cellana* spp., *Melagraphia aethiops*, *Haliotis iris*, *Chiton pelliserpentis*, *Pateloidea* spp. and *Cantharidus* spp. were found at the study sites they were not abundant ( $<1 \text{ per m}^{-2}$ ) and are likely to have had a negligible effect on survival of embryonic sporophytes. Further experiments at large spatial scales are needed to determine the site specific effects of grazing on survival of embryonic sporophytes of *U. pinnatifida*.

### Competition

The arrival of a strongly competitive, invasive species to a foreign shore means that interactions with native species are likely to be intense unless an unoccupied niche is available. Initial studies of *U. pinnatifida* populations around New Zealand found that the alga already occupied areas from the subtidal fringe to depths of 7-9 m (Hay and Lukens 1987; Brown and Lamare 1994). At Stewart Island, plants can be found to a depth of 15 m (Dr Michael Stuart *pers comm.*). Previous studies have suggested that *U. pinnatifida* may compete for space with other large laminarian and fucalean species, which dominate the New Zealand coastline (Hay and Luckens 1987; Hay and Villouta 1993). Fucalean species, including *Carpophyllum* spp., *Marginariella* spp., *Landsburgia quercifolia* and *Sargassum* spp. dominate the coast line of New Zealand from the mid intertidal to depths of 8m (Schiel 1988& 1990), whereas the few laminarian species, which include *M. pyrifera*, *Ecklonia radiata* and *Lessonia variegata*, are subtidal and generally form discontinuous stands (Choat and Schiel 1982; Hay 1990; Schiel 1990; Schiel and Nelson 1990).

Hay and Villouta (1993) suggested that because most large brown seaweeds in New Zealand are perennial, *U. pinnatifida* may invade their habitat when areas are cleared by disturbance. In Tasmania, removal of the native algal canopy was found to be critical for the establishment of *U. pinnatifida* (Valentine and Johnson 2003). However, after a period of two years, *U. pinnatifida* abundance declined significantly within the cleared treatments because the native canopy-forming species recovered. My experiments that examined canopy disturbance within *C. maschalocarpum* showed that *U. pinnatifida* is very effective at recruiting quickly after a disturbance and probably relies on the presence of embryonic sporophytes present beneath the canopy. However, because *U. pinnatifida* is an annual species and generally does not recruit in summer, it lacks the ability to persist in areas over longer periods, especially smaller areas (< 25 x 25 cm). Instead, the perennial life history of *C. maschalocarpum* and the fact that it recruits during the summer, allows it to regenerate slowly but steadily over time. *Undaria pinnatifida* is probably effective at “grabbing” space during winter when heavy wave action and storms can remove sections of canopy. However, it is unlikely to “grab” space following a disturbance in summer due to its inability to recruit during this season.

Although my study focused on the competitive ability of *U. pinnatifida* to encroach into areas dominated by large habitat forming canopy species (*C. maschalocarpum*), *Undaria pinnatifida* occupies areas slightly higher in the intertidal than *C. maschalocarpum*. Thus, it is possible that the strongest competitive interactions would be with other species of seaweeds that are found at a similar tidal height. Hay and Villouta (1993) noted that *U. pinnatifida* displaced small red and green foliose species along a breakwater in southern New Zealand. Therefore, future studies on competition might focus on some of the smaller species that occupy a similar tidal height to *U. pinnatifida*. However, assessing the full impact of *U. pinnatifida* on these species may be difficult as many of the them are not numerically dominant. Furthermore, many of these species are either undescribed, or their life histories are poorly understood.

### Summary

There are relatively few intertidal laminarians worldwide. Those that do occur intertidally have a range of morphological, demographic and physiological characteristics that enable them to persist. For example, *Hedophyllum sessile*, which inhabits semi-exposed areas of the north-east Pacific, persists due its strong holdfast and leathery blades that keep it from being removed or damaged during periods of bad weather (Markel and DeWreede 1998; Milligan and DeWreede 2000). If blades are damaged it has the ability to regenerate blade tissue as long as the holdfast and meristem are still present (Armstrong 1987). In contrast, the biennial kelp *Alaria marginata* occupies moderately sheltered to wave-exposed areas along the west coast of North America. These plants are typically found in patches a few decimeters in diameter with several patches making up a stand (Kusomo and Druehl 2000). The fact that these plants form dense patches and occupy areas with continual wave splash, probably provides relief from desiccation for this species during periods of exposure during low tide. Compared with *H. sessile* and *A. marginata*, the most significant characteristics enabling *U. pinnatifida* to persist intertidally are its large reproductive output, a bi-annual life history, the facilitation of recruitment by coralline turfs and the ability of embryonic sporophytes to persist during unfavourable recruitment periods.

The worldwide spread of *U. pinnatifida* has been closely associated with human activities (Hay and Luckens 1987; Hay 1990; Sanderson and Barrett 1990; Floc'h *et al.* 1991; Casas and Piriz 1994; Fletcher and Manfredi 1995; Curiel *et al.* 1998), and much is known about its larger scale dispersal mechanisms. However, very little has been reported on local-scale processes which make *U. pinnatifida* an increasingly common and successful invader of temperate marine ecosystems. In this thesis I have identified some of the key processes and mechanisms involved in the successful establishment and persistence of *U. pinnatifida* within intertidal habitats in southern New Zealand (Fig. 6.2). First, the species exerts enormous propagule pressure on local habitats because of its high reproductive output per plant, an extended reproductive period, and its probable ability to complete two generations in one year. Second, recruitment is facilitated by coralline turfs within the intertidal zone. Finally, embryonic sporophytes have the ability to delay recruitment in

unfavourable conditions. In contrast, grazing is seen as a minor factor in the population ecology of this plant whereas encroachment of *U. pinnatifida* may be inhibited by competition with large canopy forming species (Fig. 6.2).

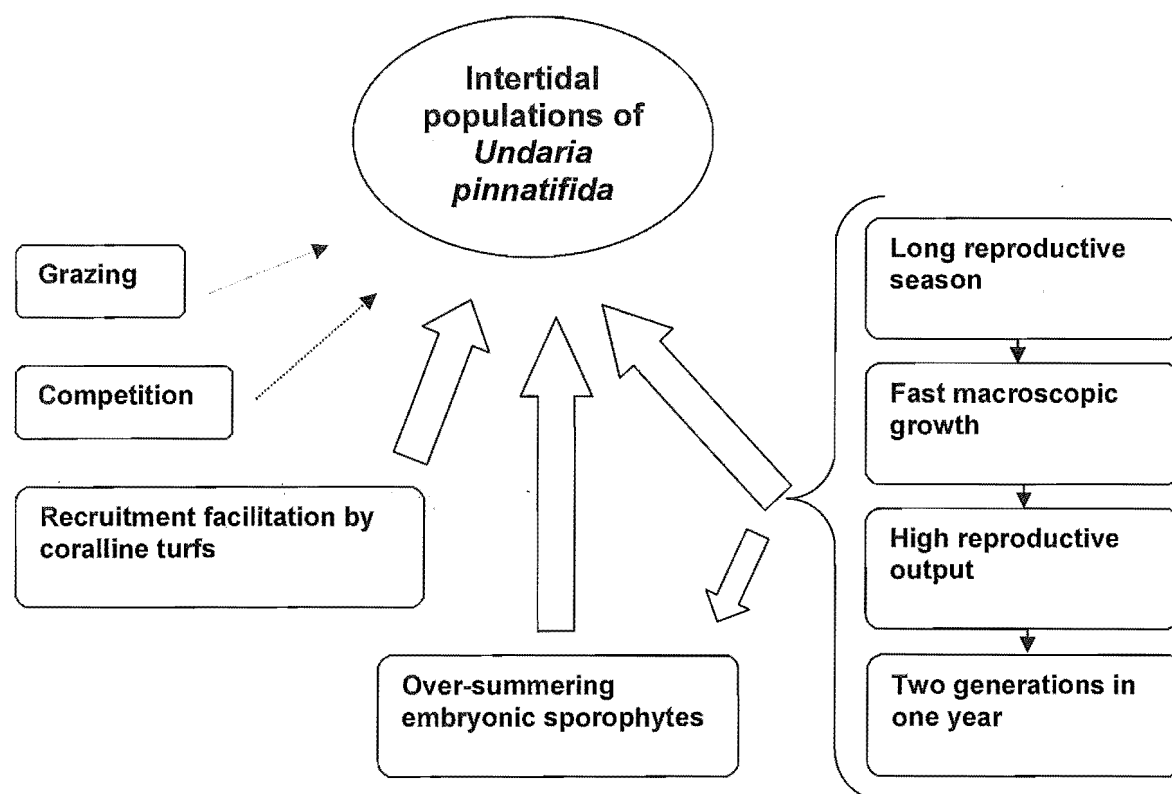


Figure 6.2: Flow diagram summarising the factors studied in this thesis and the relative importance of each factor (denoted by thickness of arrow).

# References

- Adams, N. (1994). *Seaweeds of New Zealand: An illustrated guide*. Canterbury University Press, Christchurch.
- Airoidi, L. (1998). Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. *Ecology* **79**(8): 2759-2770.
- Airoidi, L. (2000). Responses of algae with different life histories to temporal and spatial variability of disturbance in subtidal reefs. *Marine Ecology Progress Series* **195**: 81-92.
- Airoidi, L. (2003). The effects of sedimentation on rocky coast assemblages. *Oceanography and Marine Biology: An Annual Review* **41**:161-236.
- Airoidi, L., Fabiano, M., and Cinelli, F. (1996). Sediment deposition and movement over a turf assemblage in a shallow rocky coastal area of the Ligurian Sea. *Marine Ecology Progress Series* **133**(1-3): 241-251.
- Akiyama, K. (1965). Studies of ecology and culture of *Undaria pinnatifida* (Harv.)  
Sur. II. Environmental factors affecting the growth and maturation of gametophyte. *Bulletin of Tohoku Regional Fisheries Research Laboratory* **25**: 143-170.
- Ambrose, R. F., and Nelson, B. V. (1982). Inhibition of giant kelp recruitment by an introduced brown alga. *Botanica Marina* **115**: 265-267.
- Anderson, R. J., Carrick, P., Levitt, G. J., and Share, A. (1997). Holdfasts of adult kelp *Ecklonia maxima* provide refuges from grazing for recruitment of juvenile kelps. *Marine Ecology Progress Series* **159**: 265-273.
- Anderson, E. K., and North, W. J. (1969). Light requirements of juvenile and microscopic stages of giant kelp *Macrocystis*. *Proceedings of the International Seaweed Symposium* **6**: 3-15.
- Ang, P. O., and De Wreede, R. E. (1992). Density-dependence in a population of *Fucus distichus*. *Marine Ecology Progress Series* **90**: 169-181.
- Arakawa, H., and Matsuike, K. (1992). Influence on insertion of zoospores, germination, survival, and maturation of gametophytes of brown algae exerted by sediments. *Nippon Suisan Gakkaishi* **58**(4): 619-625.
- Armstrong, S. L. (1987). Mechanical properties of the tissues of the brown alga *Hedophyllum sessile* (C Ag) Setchell: variability with habitat. *Journal of Experimental Marine Biology and Ecology* **114**(2-3): 143-151.



- Baker, H. G. (1974). The evolution of weeds. *Annual review of ecological systematics* **5**: 1-24.
- Bell, E.C. and Denny, M.W. (1994). Quantifying "wave exposure": a simple device for recording maximum velocity and results of its use at several field sites. *Journal of Experimental Marine Biology and Ecology* **181**: 9-29.
- Bellan-Santini, D., Arnaud, P. M., Bellan, G., and Verlaque, M. (1996). The influence of the introduced tropical alga *Caulerpa taxifolia*, on the biodiversity of the Mediterranean marine biota. *Journal of the Marine Biological Association of the United Kingdom* **76(1)**: 235-237.
- Benedetti-Cecchi, L., and Cinelli, F. (1992). Effects of canopy cover, herbivores and substratum type on patterns of *Cystoseira* spp. settlement and recruitment in littoral rockpools. *Marine Ecology Progress Series* **90(2)**: 183-191.
- Benedetti-Cecchi, L., and Cinelli, F. (1993). Early patterns of algal succession in a midlittoral community of the Mediterranean Sea: a multifactorial experiment. *Journal of Experimental Marine Biology and Ecology* **169(1)**: 15-31.
- Benedetti-Cecchi, L., and Cinelli, F. (1994). Recovery of patches in an assemblage of geniculate coralline algae: variability at different successional stages. *Marine Ecology Progress Series* **110(1)**: 9-8.
- Berlow, E. L. (1997). From canalization to contingency: historical effects in a successional rocky intertidal community. *Ecological Monographs* **67(4)**: 435-460.
- Black, R. (1974). Some biological interactions affecting intertidal populations of the kelp *Egregia laevis*. *Marine Biology* **28(3)**: 189-198.
- Blanchette, C. A. (1996). Seasonal patterns of disturbance influence recruitment of the sea palm, *Postelsia palmaeformis*. *Journal of Experimental Marine Biology and Ecology* **197(1)**: 1-14.
- Boalch, G. T., and Potts, G. W. (1977). 1st occurrence of *Sargassum muticum* (Yendo) Fensholt in Plymouth Area. *Journal of the Marine Biological Association of the United Kingdom* **57(1)**: 29-31.
- Bolton, J. J., and Levitt, G. J. (1985). Light and temperature requirements for growth and reproduction in gametophytes of *Ecklonia maxima* (Alariaceae, Laminariales). *Marine Biology* **87(2)**: 131-135.

- Boudouresque, C. F., Meinesz, A., Ribera, M. A., and Ballesteros, E. (1995).** Spread of the green alga *Caulerpa taxifolia* (Caulerpales, Chlorophyta) in the Mediterranean: possible consequences of a major ecological event. *Scientia Marina* **59**: 21-29.
- Brawley, S. H., and Johnson, L. E. (1991).** Survival of fucoid embryos in the intertidal zone depends upon developmental stage and microhabitat. *Journal of Phycology* **27(2)**: 179-186.
- Brawley, S. H., and Johnson, L. E. (1993).** Predicting desiccation stress in microscopic organisms: the use of agarose beads to determine evaporation within and between intertidal microhabitats. *Journal of Phycology* **29(4)**: 528-535.
- Brown, M. T., and Lamare, M. D. (1994).** The distribution of *Undaria pinnatifida* (Harvey) Suringer within Timaru harbour, New Zealand. *Japanese Journal of Phycology (Sorui)* **42**: 63-70.
- Brown, R. L., and Peet, R. K. (2003).** Diversity and invasibility of southern Appalachian plant communities. *Ecology* **84(1)**: 32-39.
- Bruno, J. F. (2000).** Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. *Ecology* **81(5)**: 1179-1192.
- Bruno, J. F., and Kennedy, C. W. (2000).** Patch-size dependent habitat modification and facilitation on New England cobble beaches by *Spartina alterniflora*. *Oecologia* **122(1)**: 98-108.
- Bruno, J. F., Stachowicz, J. J., and Bertness, M. D. (2003).** Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution* **18(3)**: 119-125.
- Buggeln, R. G. (1974).** Physiological investigations on *Alaria esculenta* (L.) Grev. (Laminariales). I. Elongation of the blade. *Journal of Phycology* **10**: 283-288.
- Campbell, S. J., Bite, J. S., and BurrIDGE, T. R. (1999).** Seasonal patterns in the photosynthetic capacity, tissue pigment and nutrient content of different developmental stages of *Undaria pinnatifida* (Phaeophyta: Laminariales) in Port Phillip Bay south-eastern Australia. *Botanica Marina* **42(3)**: 231-241.
- Campbell, S. J., and BurrIDGE, T. R. (1998).** Occurrence of *Undaria pinnatifida* (Phaeophyta: Laminariales) in Port Phillip Bay, Victoria, Australia. *Marine and Freshwater Research* **49(5)**: 379-381.

- Camus, P. A.** (1994). Recruitment of the intertidal kelp *Lessonia nigrescens* Bory in Northern Chile: successional constraints and opportunities. *Journal of Experimental Marine Biology and Ecology* **184**(2): 171-181.
- Carlton, J. T.** (1989). Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. *Conservation Biology* **3**(3): 265-273.
- Carlton, J. T.** (1996). Pattern, process, and prediction in marine invasion ecology. *Biological Conservation* **78**(1-2): 97-106.
- Carlton, J. T., and Geller, J. B.** (1993). Ecological roulette: The global transport of nonindigenous marine organisms. *Science Washington D C* **261**(5117): 78-82.
- Casas, G. N., and Piriz, M. L.** (1996). Surveys of *Undaria pinnatifida* (Laminariales, Phaeophyta) in Golfo Nuevo, Argentina. *Hydrobiologia* **326/327**: 213-215.
- Castric-Fey, A., Beaupoil, C., Bouchain, J., Pradier, E., and L'Hardy-Halos, M. T.** (1999a). The introduced alga *Undaria pinnatifida* (Laminariales, Alariaceae) in the rocky shore ecosystem of the St Malo area: Growth rate and longevity of the sporophyte. *Botanica Marina* **42**(1): 83-96.
- Castric-Fey, A., Beaupoil, C., Bouchain, J., Pradier, E., and L'Hardy-Halos, M. T.** (1999b). The introduced alga *Undaria pinnatifida* (Laminariales, Alariaceae) in the rocky shore ecosystem of the St Malo area: Morphology and growth of the sporophyte. *Botanica Marina* **42**(1): 71-82.
- Castric-Fey, A., Girard, A., and L'Hardy-Halos, M. T.** (1993). The distribution of *Undaria pinnatifida* (Phaeophyceae, Laminariales) on the coast of St Malo (Brittany, France). *Botanica Marina* **36**(4): 351-358.
- Ceccherelli, G., and Cinelli, F.** (1998). Habitat effect on spatio-temporal variability in size and density of the introduced alga *Caulerpa taxifolia*. *Marine Ecology Progress Series* **163**: 289-294.
- Ceccherelli, G., and Cinelli, F.** (1999). The role of vegetative fragmentation in dispersal of the invasive alga *Caulerpa taxifolia* in the Mediterranean. *Marine Ecology Progress Series* **182**: 299-303.
- Ceccherelli, G., and Piazzzi, L.** (2001). Dispersal of *Caulerpa racemosa* fragments in the Mediterranean: lack of detachment time effect on establishment. *Botanica Marina* **44**(3): 209-213.

- Ceccherelli, G., Piazzì, L., and Balata, D. (2002). Spread of introduced *Caulerpa* species in macroalgal habitats. *Journal of Experimental Marine Biology and Ecology* **280**(1-2): 1-11.
- Cecere, E., Petrocelli, A., and Saracino, O. D. (2000). *Undaria pinnatifida* (Fucophyceae, Laminariales) spread in the central Mediterranean: its occurrence in the Mar Piccolo of Taranto (Ionian Sea, southern Italy). *Cryptogamie Algologie* **21**(3): 305-309.
- Chapman, A. R. O. (1984a). Population and community ecology of seaweeds.
- Chapman, A. R. O. (1984b). Reproduction, recruitment and mortality in two species of *Laminaria* Lamour in south-west Nova Scotia. *British Phycological Journal* **19**(2): 191-191.
- Chapman, A. R. O. (1986). Age versus stage: an analysis of age and size specific mortality and reproduction in a population of *Laminaria longicruris*. *Journal of Experimental Marine Biology and Ecology* **97**: 113-122.
- Chapman, A. R. O., and Burrows, E. M. (1970). Experimental investigations into the controlling effects of light conditions on the development and growth of *Desmarestia ligulata* (L.) Lamour. *Phycologia* **9**(1): 103-108.
- Chapman, A. R. O., and Craigie, J. S. (1977). Seasonal growth in *Laminaria longicruris*: Relations with dissolved inorganic nutrients and internal reserves of nitrogen. *Marine Biology* **40**(3): 197-205.
- Choat, J. H., and Schiel, D. R. (1982). Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. *Journal of Experimental Marine Biology and Ecology* **60**(2-3): 129-162.
- Clayton, M. N. (1988). Evolution and life histories of brown algae. *Botanica Marina* **31**(5): 379-387.
- Connell, S. D. (2003). Negative effects overpower the positive of kelp to exclude invertebrates from the understorey community. *Oecologia* **137**(1): 97-103.
- Connell, J. H., Lowman, M. D., and Noble, I. R. (1997). Subcanopy gaps in temperate and tropical forests. *Australian Journal of Ecology* **22**(2): 163-168.
- Connell, J. H., and Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**(982): 1119-1144.

- Coyer, J. A., and Zaugg-haglund, A. C. (1982). A demographic study of the elk kelp, *Pelagophycus porra* (Laminariales, Lessoniaceae), with notes on *Pelagophycus* x *Macrocystis* hybrids. *Phycologia* **21**(3): 399-407.
- Crawley, M. J. (1987a). Plant ecology defended. *Trends in Ecology & Evolution* **2**(10): 304-304.
- Crawley, M. J. (1987b). What makes a community invisable? In Colonization, succession, and stability: the 26th Symposium of the British Ecological Society held jointly with the Linnean Society of London. (eds Gray A.J., Crawley, M. J., and Edwards, P.J.). Blackwell Scientific Publications, Oxford: 429-453
- Creed, J. C., Norton, T. A., and Kain, J. M. (1996). Are neighbours harmful or helpful in *Fucus vesiculosus* populations? *Marine Ecology Progress Series* **133**(1-3): 191-201.
- Critchley, A. T. (1983a). *Sargassum muticum*: a morphological description of euorpean material. *Journal of the Marine Biological Association of the United Kingdom*. **63**: 813-824.
- Critchley, A. T. (1983b). *Sargassum muticum* - a taxonomic history including world wide and western Pacific distributions. *Journal of the Marine Biological Association of the United Kingdom* **63**: 617-625.
- Critchley, A. T., Farnham, W. F., and Morrell, S. L. (1983). A chronology of new European sites of attachment for the invasive brown alga, *Sargassum muticum*, 1973-1981. *Journal of the Marine Biological Association of the United Kingdom* **63**(4):799-811.
- Critchley, A. T., Farnham, W. F., Yoshida, T., and Norton, T. A. (1990). A bibliography of the invasive alga *Sargassum muticum* (Yendo) Fensholt (Fucales, Sargassaceae). *Botanica Marina* **33**(6): 551-562.
- Curiel, D., Bellemo, G., Marzocchi, M., Scattolin, M., and Parisi, G. (1998). Distribution of introduced Japanese macroalgae *Undaria pinnatifida*, *Sargassum muticum* (Phaeophyta) and *Antithamnion pectinatum* (Rhodophyta) in the Lagoon of Venice. *Hydrobiologia* **385**: 17-22.
- Curiel, D., Guidetti, P., Bellemo, G., Scattolin, M., and Marzocchi, M. (2001). The introduced alga *Undaria pinnatifida* (Laminariales, Alariaceae) in the lagoon of Venice. *Hydrobiologia* **477**(1-3): 209-219.

- Daehler, C. C., and Strong, D. R.** (1996). Status, prediction and prevention of introduced cordgrass *Spartina* spp invasions in Pacific estuaries, USA. *Biological Conservation* **78**(1-2): 51-58.
- Darwin, C. S.** (1859). *The origin of species*. Dutton, London.
- Davis, M. A., Grime, J. P., and Thompson, K.** (2000). Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**(3): 528-534.
- Davis, M. A., Wrage, K. J., and Reich, P. B.** (1998). Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *Journal of Ecology* **86**(4): 652-661.
- Davison, I. R., and Pearson, G. A.** (1996). Stress tolerance in intertidal seaweeds. *Journal of Phycology* **32**(2): 197-211.
- Dawson, A. E. E.** (1940). Studies in the Fucales of New Zealand II. Observations on the female frond of *Carpophyllum flexuosum* (Esp.) Grev.= *Carpophyllum phyllanthus* (Turn.) Hook. and Harv. *The New Phytologist* **34**(3): 283-302.
- Dayton, P. K.** (1973). Dispersion, dispersal and persistence of the annual intertidal alga, *Postelsia palmaeformis* Ruprecht. *Ecology* **54**(2): 433-438.
- Dayton, P. K.** (1974). Competition, disturbance, and community organisation: The provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**(1): 351-389.
- Dayton, P. K.** (1975). Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs* **45**(2): 137-159.
- Dayton, P. K.** (1985). The structure and regulation of some South American kelp communities. *Ecological Monographs* **55**(4): 447-468.
- Dayton, P. K., Currie, V., Gerrodette, T., Keller, B. D., Rosenthal, R., and Ventresca, D.** (1984). Patch dynamics and stability of some California kelp communities. *Ecological Monographs* **54**(3): 253-289.
- Dayton, P. K., Tegner, M. J., Parnell, P. E., and Edwards, P. B.** (1992). Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecological Monographs* **62**(3): 421-445.
- Dean, T. A., Thies, K., and Lagos, S. L.** (1989). Survival of juvenile giant kelp: the effects of demographic factors, competitors, and grazers. *Ecology* **70**(2): 483-495.

- de Villèle, X., and Verlaque, M. (1995). Changes and degradation in a *Posidonia oceanica* bed invaded by the introduced tropical alga *Caulerpa taxifolia* in the north-western Mediterranean. *Botanica Marina* **38(1)**: 79-87.
- Devlinny, J. S., and Volse, L. A. (1978). Effects of sediments on development of *Macrocystis pyrifera* gametophytes. *Marine Biology* **48(4)**: 343-348.
- Deysher, L., and Norton, T. A. (1982). Dispersal and colonization in *Sargassum muticum* (Yendo) Fensholt. *Journal of Experimental Marine Biology & Ecology* **56**: 179-195.
- Deysher, L. E. (1984). Reproduction phenology of newly introduced populations of the brown alga, *Sargassum muticum* (Yendo) Fensholt. *Hydrobiologia* **116/117**: 403-407.
- Deysher, L. E., and Dean, T. A. (1986). *In situ* recruitment of sporophytes of the giant kelp, *Macrocystis pyrifera* (L) Agardh, C.A.: effects of physical factors. *Journal of Experimental Marine Biology and Ecology* **103(1-3)**: 41-63.
- Di Castri, F., Hansen, A. J., and Debussche, M. (1990). *Biological invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Druehl, L. D. (1973). Marine transplantations. *Science* **179**:12.
- Dudgeon, S. R., Steneck, R. S., Davison, I. R., and Vadas, R. L. (1999). Coexistence of similar species in a space limited intertidal zone. *Ecological Monographs* **69(3)**: 331-352.
- Duffy, J. E., and Hay, M. E. (2000). Strong impacts of grazing amphipods on the organization of a benthic community. *Ecological Monographs* **70(2)**: 237-263.
- Duggins, D. O. (1980). Kelp beds and sea otters: an experimental approach. *Ecology* **61(3)**: 447-453.
- Dumay, O., Fernandez, C., and Pergent, G. (2002). Primary production and vegetative cycle in *Posidonia oceanica* when in competition with the green algae *Caulerpa taxifolia* and *Caulerpa racemosa*. *Journal of the Marine Biological Association of the United Kingdom* **82(3)**: 379-387.
- Duncan, R. P., Blackburn, T. M., and Sol, D. (2003). The ecology of bird species. *Annual Review of Ecology, Evolution, and Systematics*. **34**: 71-98.

- Edwards, M. S. (1998). Effects of long-term kelp canopy exclusion on the abundance of the annual alga *Desmarestia ligulata* (Light F). *Journal of Experimental Marine Biology and Ecology* **228**(2): 309-326.
- Edwards, M. S. (2000). The role of alternate life history stages of a marine macroalga: A seed bank analogue? *Ecology* **81**(9): 2404-2415.
- Elton, C. S. (1958). *The ecology of invasions by animals and plants*. London : Methuen.
- Farnham, W. F., Fletcher, R.L. and Irvine, L.M. (1973). Attached *Sargassum* found in Britain. *Nature* **243**: 231-232.
- Farrell, T. M. (1989). Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. *Journal of Experimental Marine Biology and Ecology* **128**(1): 57-73.
- Fernández, C., Gutiérrez, L. M., and Rico, J. M. (1990). Ecology of *Sargassum muticum* on the north coast of Spain: preliminary observations. *Botanica Marina* **33**(5): 423-428.
- Fletcher, R. L. (1980). Studies on the recently introduced brown alga *Sargassum muticum* (Yendo) Fensholt .3. Periodicity in gamete release and incubation of early germling stages. *Botanica Marina* **23**(7): 425-432.
- Fletcher, R. L., and Farrell, P. (1998). Introduced brown algae in the north east Atlantic, with particular respect to *Undaria pinnatifida* (Harvey) Suringar. *Helgolander Meeresuntersuchungen* **52**(3-4): 259-275.
- Fletcher, R. L., and Manfredi, C. (1995). The occurrence of *Undaria pinnatifida* (Phaeophyceae, Laminariales) on the south coast of England. *Botanica Marina* **38**(4): 355-358.
- Floc'h, J. Y., Pajot, R., and Wallentinus, I. (1991). The Japanese brown alga *Undaria pinnatifida* on the coast of France and its possible establishment in European waters. *Journal Du Conseil* **47**(3): 379-390.
- Floch, J. Y., Pajot, R., and Mouret, V. (1996). *Undaria pinnatifida* (Laminariales, Phaeophyta) 12 years after its introduction into the Atlantic Ocean. *Hydrobiologia* **327**: 217-222.



- Flores-Moya, A., Fernández, J. A., and Niell, F. X. (1993). Reproductive phenology, growth and primary production of *Phyllariopsis purpurascens* (Phyllariaceae, Phaeophyta) from the Straits of Gibraltar. *European Journal of Phycology* **28**: 223-230.
- Flores-Moya, A., Fernandez, J. A., and Niell, F. X. (1996). Growth pattern, reproduction, and self-thinning in seaweeds. *Journal of Phycology* **32**: 767-769.
- Forrest, B. M., Brown, S. N., Taylor, M. D., Hurd, C. L., and Hay, C. H. (2000). The role of natural dispersal mechanisms in the spread of *Undaria pinnatifida* (Laminariales, Phaeophyceae). *Phycologia* **39**(6): 547-553.
- Foster, M. S. (1975). Algal succession in a *Macrocystis pyrifera* forest. *Marine Biology* **32**(4): 313-329.
- Foster, M. S. (1982). Factors controlling the intertidal zonation of *Iridaea flaccida* (Rhodophyta). *Journal of Phycology* **18**(2): 285-294.
- Gagné, J. A., Mann, K. H., and Chapman, A. R. O. (1982). Seasonal patterns of growth and storage in *Laminaria longicruris* in relation to differing patterns of availability of nitrogen in the water. *Marine Biology* **69**: 91-101.
- Gavio, B., and Fredericq, S. (2002). *Grateloupia turuturu* (Halymeniaceae, Rhodophyta) is the correct name of the non-native species in the Atlantic known as *Grateloupia doryphora*. *European Journal of Phycology* **37**(3): 349-359.
- Gendron, L. (1989). Seasonal growth of the kelp *Laminaria longicruris* in Baie des Chaleurs, Québec, in relation to nutrient and light availability. *Botanica Marina* **32**(4): 345-354.
- Gerard, V. A., and Mann, K. H. (1979). Growth and production of *Laminaria longicruris* (Phaeophyta) populations exposed to different intensities of water movement. *Journal of Phycology* **15**(1): 33-41.
- Gibbons, M. J. (1988). The impact of sediment accumulations, relative habitat complexity and elevation on rocky shore meiofauna. *Journal of Experimental Marine Biology and Ecology* **122**(3): 225-241.
- Gibbs, M., Ross, A., and Downes, M. (2002). Nutrient cycling and fluxes in Beatrix Bay, Pelorus Sound, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **36**: 675-697.

- Graham, M. H. (1997). Factors determining the upper limit of giant kelp, *Macrocystis pyrifera* Agardh, along the Monterey Peninsula, central California, USA. *Journal of Experimental Marine Biology and Ecology* **218**(1): 127-149.
- Grosholz, E. (2002). Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology & Evolution* **17**(1): 22-27.
- Grosholz, E. D., and Ruiz, G. M. (1995). Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in Central California. *Marine Biology* **122**(2): 239-247.
- Hales, J. M., and Fletcher, R. L. (1990). Studies on the recently introduced brown alga *Sargassum muticum* (Yendo) Fensholt .5. Receptacle initiation and growth, and gamete release in laboratory culture. *Botanica Marina* **33**(3): 241-249.
- Harlin, M. M., and Villalard-Bohnsack, M. (2001). Seasonal dynamics and recruitment strategies of the invasive seaweed *Grateloupia doryphora* (Halymeniaceae, Rhodophyta) in Narragansett Bay and Rhode Island Sound, Rhode Island, USA. *Phycologia* **40**(5): 468-474.
- Harris, L. G., Ebeling, A. W., Laur, D. R., and Rowley, R. J. (1984). Community recovery after storm damage: a case of facilitation in primary succession. *Science* **224**(4655): 1336-1338.
- Harrold, C., and Reed, D. C. (1985). Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* **66**(4): 1160-1169.
- Hay, C. H. (1990). The dispersal of sporophytes of *Undaria pinnatifida* by coastal shipping in New Zealand, and implications for further dispersal of *Undaria* in France. *British Phycological Journal* **25**(4): 301-314.
- Hay, C. H., and Luckens, P. A. (1987). The Asian kelp *Undaria pinnatifida* (Phaeophyta, Laminariales) found in a New Zealand harbor. *New Zealand Journal of Botany* **25**(2): 329-332.
- Hay, C. H., and Villouta, E. (1993). Seasonality of the adventive Asian kelp *Undaria pinnatifida* in New Zealand. *Botanica Marina* **36**: 461-476.
- Hengeveld, R. (1989). *Dynamics of biological invasions*. Chapman and Hall, London.
- Hobbs, R. J., and Mooney, H. A. (1991). Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology* **72**(1): 59-68.

- Hoffmann, A. J., and Santelices, B. (1991). Banks of algal microscopic forms: hypotheses on their functioning and comparisons with seed banks. *Marine Ecology Progress Series* **79(1-2)**: 185-194.
- Hruby, T., and Norton, T. A. (1979). Algal colonization on rocky shores in the Firth of Clyde. *Journal of Ecology* **67(1)**: 65-77.
- Jenkins, S. R., Hawkins, S. J., and Norton, T. A. (1999a). Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered intertidal community. *Marine Ecology Progress Series* **188**: 81-92.
- Jenkins, S. R., Hawkins, S. J., and Norton, T. A. (1999b). Interaction between a fucoid canopy and limpet grazing in structuring a low shore intertidal community. *Journal of Experimental Marine Biology and Ecology* **233(1)**: 41-63.
- Jernakoff, P. (1985). Interactions between the limpet *Patelloida latistrigata* and algae on an intertidal rock platform. *Marine Ecology Progress Series* **23(1)**: 71-78.
- Johnson, C. R., and Mann, K. H. (1986). The crustose coralline alga, *Phymatolithon foslíe*, inhibits the overgrowth of seaweeds without relying on herbivores. *Journal of Experimental Marine Biology and Ecology* **96(2)**: 127-146.
- Jones, G., and Farnham, W. F. (1973). Japweed: new threat to British coasts. *New Scientist* **60**: 394-395.
- Jousson, O., Pawlowski, J., Zaninetti, L., Zechman, F. W., Dini, F., Di Guiseppe, G., Woodfield, R., Millar, A., and Meinesz, A. (2000). Invasive alga reaches California: The alga has been identified that threatens to smother Californian coastal ecosystems. *Nature* **408(6809)**: 157-158.
- Kain, J. M. (1964). Aspects of the biology of *Laminaria hyperborea*. III. Survival and growth of gametophyte. *Journal of the Marine Biological Association of the United Kingdom*. **44**: 415-433.
- Kain, J. M. (1969). The biology of *Laminaria hyperborea*. V. Comparison with early stages of competitors. *Journal of Marine Biological Association of the United Kingdom*. **49**: 455-473.

- Kain, J. M. (1975). Biology of *Laminaria hyperborea*. VII. Reproduction of sporophyte. *Journal of the Marine Biological Association of the United Kingdom* **55**(3): 567-582.
- Kain, J. M. (1979). A review of the genus *Laminaria*. *Oceanography and Marine Biology: An Annual Review* **17**: 101-161.
- Keane, R. M., and Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* **17**(4): 164-170.
- Kelagher, B. P. (2002). Influence of physical characteristics of coralline turf on associated macrofaunal assemblages. *Marine Ecology Progress Series* **232**: 141-148.
- Kelagher, B. P. (2003a). Changes in habitat complexity negatively affect diverse gastropod assemblages in coralline algal turf. *Oecologia* **135**(3): 431-441.
- Kelagher, B. P. (2003b). Effects of frond length on diverse gastropod assemblages in coralline turf. *Journal of the Marine Biological Association of the United Kingdom* **83**(1): 159-163.
- Kennedy, C. W., and Bruno, J. F. (2000). Restriction of the upper distribution of New England cobble beach plants by wave-related disturbance. *Journal of Ecology* **88**(5): 856-868.
- Kennedy, T. A., Naeem, S., Howe, K. M., Knops, J. M. H., Tilman, D., and Reich, P. (2002). Biodiversity as a barrier to ecological invasion. *Nature London* **417**(6889): 636-638.
- Kennelly, S. J. (1987a). Physical disturbances in an Australian kelp community .1. temporal effects. *Marine Ecology Progress Series* **40**(1-2):145-153.
- Kennelly, S. J. (1987b). Physical disturbances in an Australian kelp community .2. Effects on understorey species due to differences in kelp cover. *Marine Ecology Progress Series* **40**(1-2): 155-165.
- Kim, J. H., and DeWreede, R. E. (1996). Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. *Marine Ecology Progress Series* **133**(1-3): 217-228.
- Kim, K. Y., Choi, T. S., Huh, S. H., and Garbary, D. J. (1998). Seasonality and community structure of subtidal benthic algae from Daedo Island, southern Korea. *Botanica Marina* **41**(4): 357-365.

- Kim, K. Y., and Lee, I. K. (1995). Community structure of subtidal macroalgae around Neobdo Island on the west southern coast of Korea. *Journal of Plant Biology* **38**(2): 153-158.
- Kimura, R. S., and Foster, M. S. (1984). The effects of harvesting *Macrocystis pyrifera* on the algal assemblage in a giant kelp forest. *Hydrobiologia* **116**: 425-428.
- Kinlan, B. P., Graham, M. H., Sala, E., and Dayton, P. K. (2003). Arrested development of giant kelp (*Macrocystis pyrifera*, Phaeophyceae) embryonic sporophytes: A mechanism for delayed recruitment in perennial kelps? *Journal of Phycology* **39**(1): 47-57.
- Klinger, T. (1993). The persistence of haplodiploidy in algae. *Trends in Ecology & Evolution* **8**: 256-258.
- Knoepffler-Peguy, M., Belsher, T., Boudouresque, C. F., and Lauret, M. (1985). *Sargassum muticum* begins to invade the Mediterranean. *Aquatic Botany* **23**(3):291-295.
- Knops, J. M. H., Tilman, D., Haddad, N. M., Naeem, S., Mitchell, C. E., Haarstad, J., Ritchie, M. E., Howe, K. M., Reich, P. B., Siemann, E., and Groth, J. (1999). Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* **2**(5): 286-293.
- Koh, C. H., and Shin, H. C. (1990). Growth and size distribution of some large brown algae in Ohori, east coast of Korea. *Hydrobiologia* **204**: 225-231.
- Kolar, C. S., and Lodge, D. M. (2001). Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* **16**(4): 199-204.
- Kusumo, H. T., and Druehl, L. D. (2000). Variability over space and time in the genetic structure of the winged kelp *Alaria marginata*. *Marine Biology* **136**(3): 397-409.
- Larkum, A. W. D. (1986). A study of growth and primary production in *Ecklonia radiata* (C-Ag) J-Agardh (Laminariales) at a sheltered site in Port Jackson, New South Wales. *Journal of Experimental Marine Biology and Ecology* **96**(2): 177-190.
- Levine, J. M., and D'Antonio, C. M. (1999). Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**(1): 15-26.

- Lodge, D. M. (1993). Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* **8**(4): 133-137.
- Lonsdale, W. M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**(5): 1522-1536.
- Lotze, H. K., and Worm, B. (2000). Variable and complementary effects of herbivores on different life stages of bloom forming macroalgae. *Marine Ecology Progress Series* **200**: 167-175.
- Lotze, H. K., Worm, B., Molis, M., and Wahl, M. (2002). Effects of UV radiation and consumers on recruitment and succession of a marine macrobenthic community. *Marine Ecology Progress Series* **243**: 57-66.
- Lüning, K. (1980). Critical light levels and temperature regulating the gametogenesis of three *Laminaria* species (Phaeophyceae). *Journal of Phycology* **16**: 1-15.
- Lüning, K., and tom Dieck, I. (1989). Environmental triggers in algal seasonality. *Botanica Marina* **32**(5): 389-397.
- Lüning, K., and Dring, M. J. (1972). Reproduction induced by blue light in female gametophytes of *Laminaria saccharina*. *Planta* **104**: 252-256.
- Lüning, K., and Neushul, M. (1978). Light and temperature demands for growth and reproduction of laminarian gametophytes in southern and central California. *Marine Biology* **45**(4): 297-309.
- Mann, E. H., and Kirkman, H. (1981). Biomass method for measuring productivity of *Ecklonia radiata*, with the potential for adaptation to other large brown algae. *Australian Journal of Marine and Freshwater Research* **32**(2): 297-304.
- Markel, R. W., and DeWreede, R. E. (1998). Mechanisms underlying the effect of the chiton *Katharina tunicata* on the kelp *Hedophyllum sessile*: size escapes and indirect effects. *Marine Ecology Progress Series* **166**: 151-161.
- Masaki, T., Fujita, D., and Hagen, N. T. (1984). The surface ultrastructure and epithellium shedding of crustose coralline algae in an isoyake area of southwestern Hokkaido, Japan. *Hydrobiologia* **116**: 218-223.
- Maxell, B. A., and Miller, K. A. (1996). Demographic studies of the annual kelps *Nereocystis luetkeana* and *Costaria costata* (Laminariales, Phaeophyta) in Puget Sound, Washington. *Botanica Marina* **39**(5): 479-489.

- Meinesz, A., Devaugelas, J., Hesse, B., and Mari, X. (1993). Spread of the introduced tropical green alga *Caulerpa taxifolia* in northern Mediterranean waters. *Journal of Applied Phycology* **5(2)**: 141-147.
- Meinesz, A., and Hesse, B. (1991). Introduction of the tropical alga *Caulerpa taxifolia* and its invasion of the north-western Mediterranean. *Oceanologica Acta* **14(4)**: 415-426.
- Milligan, K. L. D., and DeWreede, R. E. (2000). Variations in holdfast attachment mechanics with developmental stage, substratum type, season, and wave exposure for the intertidal kelp species *Hedophyllum sessile* (C. Agardh) Setchell. *Journal of Experimental Marine Biology and Ecology* **254(2)**: 189-209.
- Naeem, S., Knops, J. M. H., Tilman, D., Howe, K. M., Kennedy, T., and Gale, S. (2000). Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* **91(1)**: 97-108.
- Norton, T. A. (1969). Growth form and environment in *Saccorhiza polyschides*. *Journal of Marine Biological Association of the United Kingdom*. **49**:1025-1045.
- Norton, T. A. (1976). Why is *Sargassum muticum* so invasive? *British Phycological Journal* **11**: 197-198.
- Norton, T. A. (1977). Ecological experiments with *Sargassum muticum*. *Journal of the Marine Biological Association of the United Kingdom* **57**: 33-43.
- Novaczek, I. (1984a). Response of *Ecklonia radiata* (Laminariales) to light at 15-degrees C with reference to the field light budget at Goat Island Bay, New Zealand. *Marine Biology* **80(3)**: 263-272.
- Novaczek, I. (1984b). Response of gametophytes of *Ecklonia radiata* (Laminariales) to temperature in saturating light. *Marine Biology* **82**: 241-245.
- Oh, S. H., and Koh, C. H. (1996). Growth and photosynthesis of *Undaria pinnatifida* (Laminariales, Phaeophyta) on a cultivation ground in Korea. *Botanica Marina* **39(4)**: 389-393.
- Paine, R. T. (1979). Disaster, catastrophe, and local persistence of the sea palm *Postelsia palmaeformis*. *Science* **205(4407)**: 685-687.

- Parke, M. (1948). Studies on British Laminariaceae.I. Growth in *Laminaria saccharina* (L.) Lamour. *Journal of the Marine Biological Association of the United Kingdom* **27**: 651-709.
- Pearse, J. S., and Hines, A. H. (1979). Expansion of a central California kelp forest following the mass mortality of sea urchins. *Marine Biology* **51(1)**: 83-91.
- Perrings, C., Williamson, M. H. and Dalmazzone, S. (2000). *The economics of biological invasions*. (ed. Edward Elgar), Cheltenham.
- Pfister, C. A. (1991). Reproductive plasticity in the kelp *Alaria nana* (Phaeophyceae). *Journal of Phycology* **27(6)**: 763-766.
- Pfister, C. A. (1992). Costs of Reproduction in an intertidal kelp: patterns of allocation and life history consequences. *Ecology* **73(5)**: 1586-1596.
- Piazzi, L., Ceccherelli, G., and Cinelli, F. (2001). Threat to macroalgal diversity: effects of the introduced green alga *Caulerpa racemosa* in the Mediterranean. *Marine Ecology Progress Series* **210**: 149-159.
- Reed, D. C. (1990a). The effects of variable settlement and early competition on patterns of kelp recruitment. *Ecology* **71(2)**: 776-787.
- Reed, D. C. (1990b). An experimental evaluation of density-dependence in a subtidal algal population. *Ecology* **71(6)**: 2286-2296.
- Reed, D. C., Amsler, C. D., and Ebeling, A. W. (1992). Dispersal in kelps: factors affecting spore swimming and competence. *Ecology* **73(5)**: 1577-1585.
- Reed, D. C., Anderson, T. W., Ebeling, A. W., and Anghera, M. (1997). The role of reproductive synchrony in the colonization potential of kelp. *Ecology* **78(8)**: 2443-2457.
- Reed, D. C., Ebeling, A. W., Anderson, T. W., and Anghera, M. (1996). Differential reproductive responses to fluctuating resources in two seaweeds with different reproductive strategies. *Ecology* **77(1)**: 300-316.
- Reed, D. C., and Foster, M. S. (1984). The effects of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* **65(3)**: 937-948.
- Reed, D. C., Laur, D. R., and Ebeling, A. W. (1988). Variation in algal dispersal and recruitment: the importance of episodic events. *Ecological Monographs* **58(4)**: 321-335.



- Reed, D. C., Neushul, M., and Ebeling, A. W. (1991). Role of settlement density on gametophyte growth and reproduction in the kelps *Pterygophora californica* and *Macrocystis pyrifera* (Phaeophyceae). *Journal of Phycology* **27**(3): 361-366.
- Reed, D. C., Raimondi, P. T., Carr, M. H., and Goldwasser, L. (2000). The role of dispersal and disturbance in determining spatial heterogeneity in sedentary organisms. *Ecology* **81**(7): 2011-2026.
- Richardson, J. P. (1979). Overwintering of *Dictyota dichotoma* (Phaeophyceae) near its northern distribution limit on the east coast of North America. *Journal of Phycology* **15**(1): 22-26.
- Ruiz, G. M., Carlton, J. T., Grosholz, E. D., and Hines, A. H. (1997). Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *American Zoologist* **37**(6): 621-632.
- Ruiz, G. M., Fofonoff, P. W., Carlton, J. T., Wonham, M. J., and Hines, A. H. (2000). Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics* **31**: 481-531.
- Saito, Y. (1975). *Undaria*. in *Advances of phycology in Japan*. (eds. Tohida, J. and Hirose, H), The Hague, Junk.: 304-320.
- Sanderson, J. C. (1990). A preliminary survey of the distribution of the introduced macroalga, *Undaria pinnatifida* (Harvey) Suringer on the east coast of Tasmania, Australia. *Botanica Marina* **33**(2): 153-157.
- Sanderson, J. C., and Barrett, N. (1989). A survey of the distribution of the introduced Japanese macroalga *Undaria pinnatifida* (Harvey) Suringar on the east coast of Tasmania. Technical Report 38, Department of Sea Fisheries., Tasmania.
- Santelices, B. (1990a). Patterns of organizations of intertidal and shallow subtidal vegetation in wave exposed habitats of central Chile. *Hydrobiologia* **192**(1): 35-57.
- Santelices, B. (1990b). Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanography and Marine Biology: An Annual Review* **28**: 177-276.

- Santelices, B., and Ojeda, F. P.** (1984). Recruitment, growth and survival of *Lessonia nigrescens* (Phaeophyta) at various tidal levels in exposed habitats of central Chile. *Marine Ecology Progress Series* **19(1-2)**: 73-82.
- Schiel, D. R.** (1985a). Growth, survival and reproduction of two species of marine algae at different densities in natural stands. *Journal of Ecology* **73**: 199-217.
- Schiel, D. R.** (1985b). A short term demographic study of *Cystoseira osmundacea* (Fucales, Cystoseiraceae) in central California. *Journal of Phycology* **21(1)**: 99-106.
- Schiel, D. R.** (1988). Algal Interactions on shallow subtidal reefs in northern New Zealand: a Review. *New Zealand Journal of Marine and Freshwater Research* **22(3)**: 481-489.
- Schiel, D. R.** (1990). Macroalgal assemblages in New Zealand: structure, interactions and demography. *Hydrobiologia* **192**: 59-76.
- Schiel, D. R., and Choat, J. H.** (1980). Effects of density on monospecific stands of marine algae. *Nature* **285(5763)**: 324-326.
- Schiel, D. R., and Choat, J. H.** (1981). Micrograzers may affect macroalgal density - Reply. *Nature* **292(5819)**: 177-177.
- Schiel, D. R., and Foster, M. S.** (1986). The structure of subtidal algal stands in temperate waters. *Oceanography and Marine Biology: An Annual Review* **24**: 265-307.
- Schiel, D. R., and Nelson, W. A.** (1990). The harvesting of macroalgae in New Zealand. *Hydrobiologia* **204**: 25-33.
- Schiel, D. R., and Taylor, D. I.** (1999). Effects of trampling on a rocky intertidal algal assemblage in southern New Zealand. *Journal of Experimental Marine Biology and Ecology* **235(2)**: 213-235.
- Schonbeck, M., and Norton, T. A.** (1978). Factors controlling upper limits of fucoid algae on shore. *Journal of Experimental Marine Biology and Ecology* **31(3)**: 303-313.
- Simberloff, D., and Von Holle, B.** (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* **1**: 21-32.
- Simon, C., Gall, E. A., and Deslandes, E.** (2001). Expansion of the red alga *Grateloupia doryphora* along the coasts of Brittany (France). *Hydrobiologia* **443(1-3)**: 23-29.

- Sjøtun, K. (1993). Seasonal lamina growth in two age groups of *Laminaria saccharina* (L.) Lamour in western Norway. *Botanica Marina* **36**(5): 433-441.
- Sousa, W. P. (1979a). Disturbance in marine inter tidal boulder fields: the non-equilibrium maintenance of species diversity. *Ecology* **60**(6): 1225-1239.
- Sousa, W. P. (1979b). Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* **49**(3): 227-254.
- Sousa, W. P. (1980). The responses of a community to disturbance: the importance of successional age and species life histories. *Oecologia* **45**(1): 72-81.
- Sousa, W. P. (1984). Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. *Ecology* **65**(6): 1918-1935.
- Sousa, W. P. (1985). Disturbance and patch dynamics on rocky intertidal shores. In *The ecology of natural disturbance and patch dynamics*. (eds. Pickett T. A. and White P. S.), Academic Press, Orlando: 101-124
- Sousa, W. P., Schroeter, S. C., and Gaines, S. D. (1981). Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. *Oecologia* **48**(3): 297-307.
- Stapleton, J. C. (1988). Occurrence of *Undaria pinnatifida* (Harvey) Suringar in New Zealand. *Japanese Journal of Phycology* **36**: 178-179.
- Stohlgren, T. J., Binkley, D., Chong, G. W., Kalkhan, M. A., Schell, L. D., Bull, K. A., Otsuki, Y., Newman, G., Bashkin, M., and Son, Y. (1999). Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* **69**(1): 24-46.
- Stuart, M. D. (1997). The seasonal ecophysiology of *Undaria pinnatifida* (Harvey) Suringar in Otago Harbour, New Zealand. Ph.D. Otago University.
- Stuart, M. D., Hurd, C. L., and Brown, M. T. (1999). Effects of seasonal growth rate on morphological variation of *Undaria pinnatifida* (Alariaceae, Phaeophyceae). *Hydrobiologia* **399**: 191-199.
- Suzuki, Y., Kuma, K., Kudo, I., and Matsunaga, K. (1995). Iron requirement of the brown macroalgae *Laminaria japonica*, *Undaria pinnatifida* (Phaeophyta) and the crustose coralline alga *Lithophyllum yessoense* (Rhodophyta), and their competition in the Northern Japan Sea. *Phycologia* **34**(3): 201-205.

- Tegner, M. J., and Butler, R.A. (1985). The survival and mortality of seeded and native red abalones, *Haliotis rufescens*, on the Palos Verdes Peninsula. *California Fish and Game* **71**:150.
- Tilman, D. (1997). Distinguishing between the effects of species diversity and species composition. *Oikos* **80**(1): 185-185.
- Tilman, D., Naeem, S., Knops, J., Reich, P., Siemann, E., Wedin, D., Ritchie, M., and Lawton, J. (1997). Biodiversity and ecosystem properties. *Science* **278**(5345): 1866-1867.
- tom Dieck, I. T. (1993). Temperature tolerance and survival in darkness of kelp gametophytes (Laminariales, Phaeophyta): ecological and biogeographical implications. *Marine Ecology Progress Series* **100**(3): 253-264.
- Torchin, M. E., Lafferty, K. D., and Kuris, A. M. (1996). Infestation of an introduced host, the European green crab, *Carcinus maenas*, by a symbiotic nemertean egg predator, *Carcinonemertes epialti*. *Journal of Parasitology* **82**(3): 449-453.
- Torchin, M. E., Lafferty, K.D. and Kuris, A.M. (2001). Release from parasites as natural enemies: increased performance of a globally introduced marine crab. *Biological Invasions* **3**: 333-345.
- Trowbridge, C. D. (1995). Establishment of the green alga *Codium fragile* ssp. *tomentosoides* on New Zealand rocky shores: Current distribution and invertebrate grazers. *Journal of Ecology* **83**(6): 949-965.
- Trowbridge, C. D. (1996). Introduced versus native subspecies of *Codium fragile*: How distinctive is the invasive subspecies *tomentosoides*? *Marine Biology* **126**(2): 193-204.
- Underwood, A. J., and Jernakoff, P. (1981). Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. *Oecologia* **48**(2): 221-233.
- Vadas, R. L., Johnson, S., and Norton, T. A. (1992). Recruitment of early post-settlement stages of benthic algae. *British Phycological Journal* **27**: 331-351.
- Valentine, J. P., and Johnson, C. R. (2003). Establishment of the introduced kelp *Undaria pinnatifida* in Tasmania depends on disturbance to native algal assemblages. *Journal of Experimental Marine Biology and Ecology* **295**(1): 63-90.

- Verlaque, M., Boudouresque, C. F., Meinesz, A., and Gravez, V.** (2000). The *Caulerpa racemosa* complex (Caulerpales, Ulvophyceae) in the Mediterranean Sea. *Botanica Marina* **43**(1): 49-68.
- Vermeij, G. J.** (1996). An agenda for invasion biology. *Biological Conservation* **78**(1-2): 3-9.
- Villalard-Bohnsack, M., and Harlin, M. M.** (2001). *Grateloupia doryphora* (Halymeniaceae, Rhodophyta) in Rhode Island waters (USA): geographical expansion, morphological variations and associated algae. *Phycologia* **40**(4): 372-380.
- Vogel, S.** (1984). Drag and flexibility in sessile organisms. *American Zoology* **24**: 37-44.
- Walker, N. A.** (1998). Grazing in the intertidal zone: effects of the herbivorous *Turbo smaragdus* on macroalgal assemblages. M.Sc. University of Canterbury.
- Williamson, M.** (1996). *Biological invasions*. Chapman & Hall, London.
- Zhang, D. M., Miao, G. R., and Pei, L. Q.** (1984). Studies on *Undaria pinnatifida*. *Hydrobiologia* **116**: 263-265.

# Appendices

## Monthly size-frequency histograms

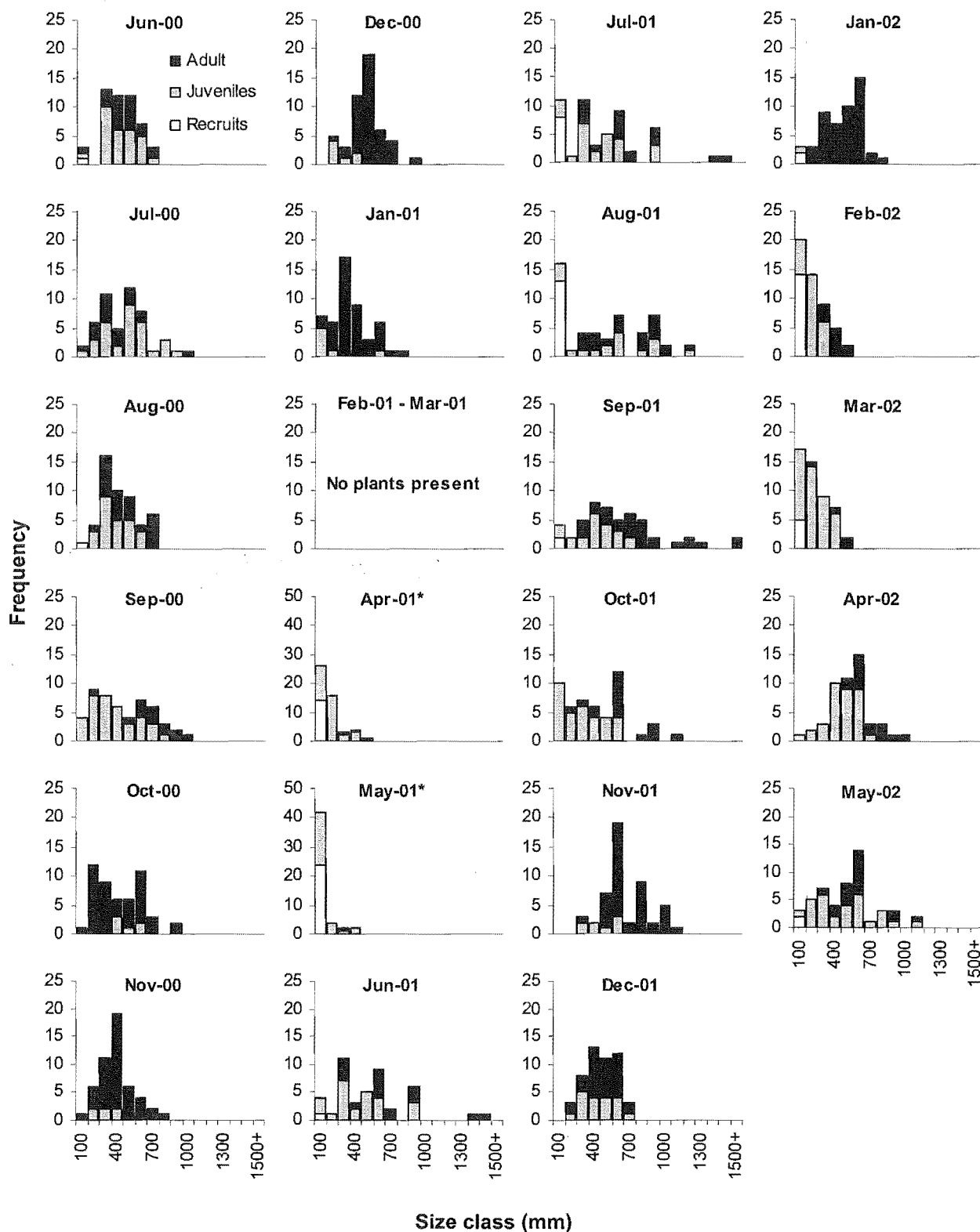


Figure A1.1: Size-frequency histograms of recruit, immature and mature *U. pinnatifida* plants from the low zone at Diamond Harbour, February 2001 and May 2002 at quarterly intervals.  $n=50$  plants each month. Shaded bars are stacked.

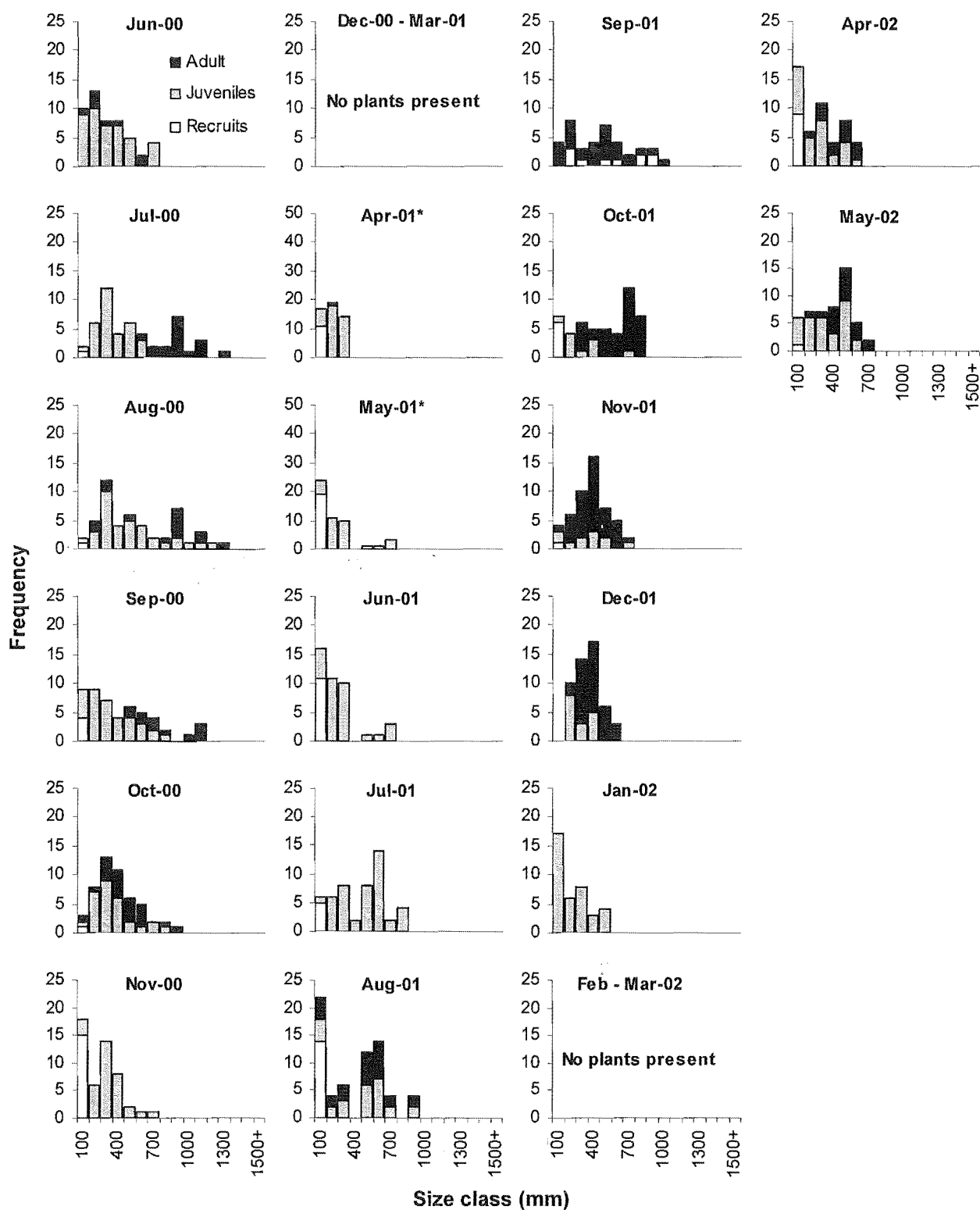


Figure A1.2: Size-frequency histograms of recruit, immature and mature *U. pinnatifida* plants from the low zone Rapaki Bay between February 2001 and May 2002 at quarterly intervals. n=50 plants each month. Shaded bars are stacked.



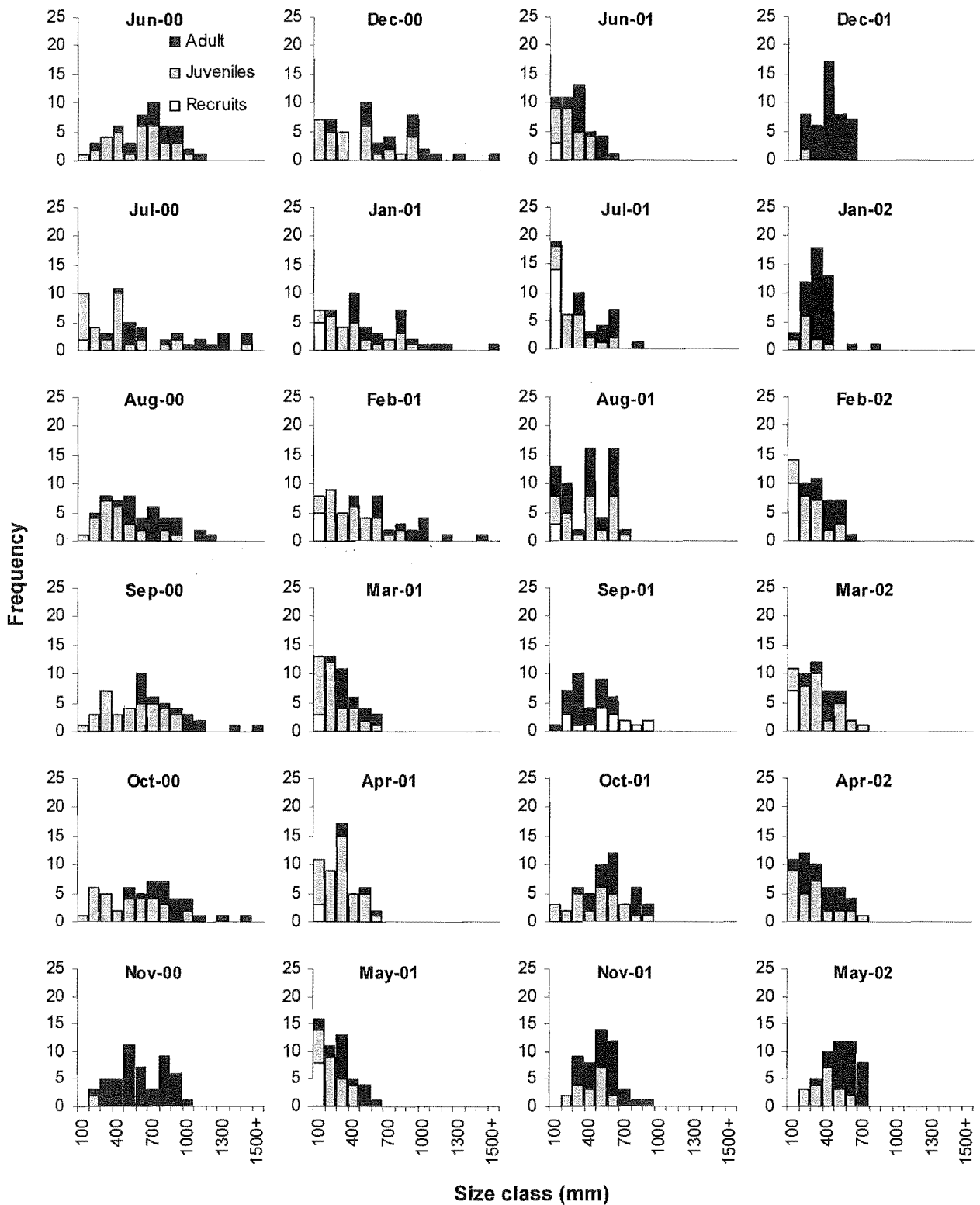


Figure A1.3: Size-frequency histograms of recruit, immature and mature *U. pinnatifida* plants from the low zone at Moeraki Beach between February 2001 and May 2002 at quarterly intervals.  $n=50$  plants each month. Shaded bars are stacked.

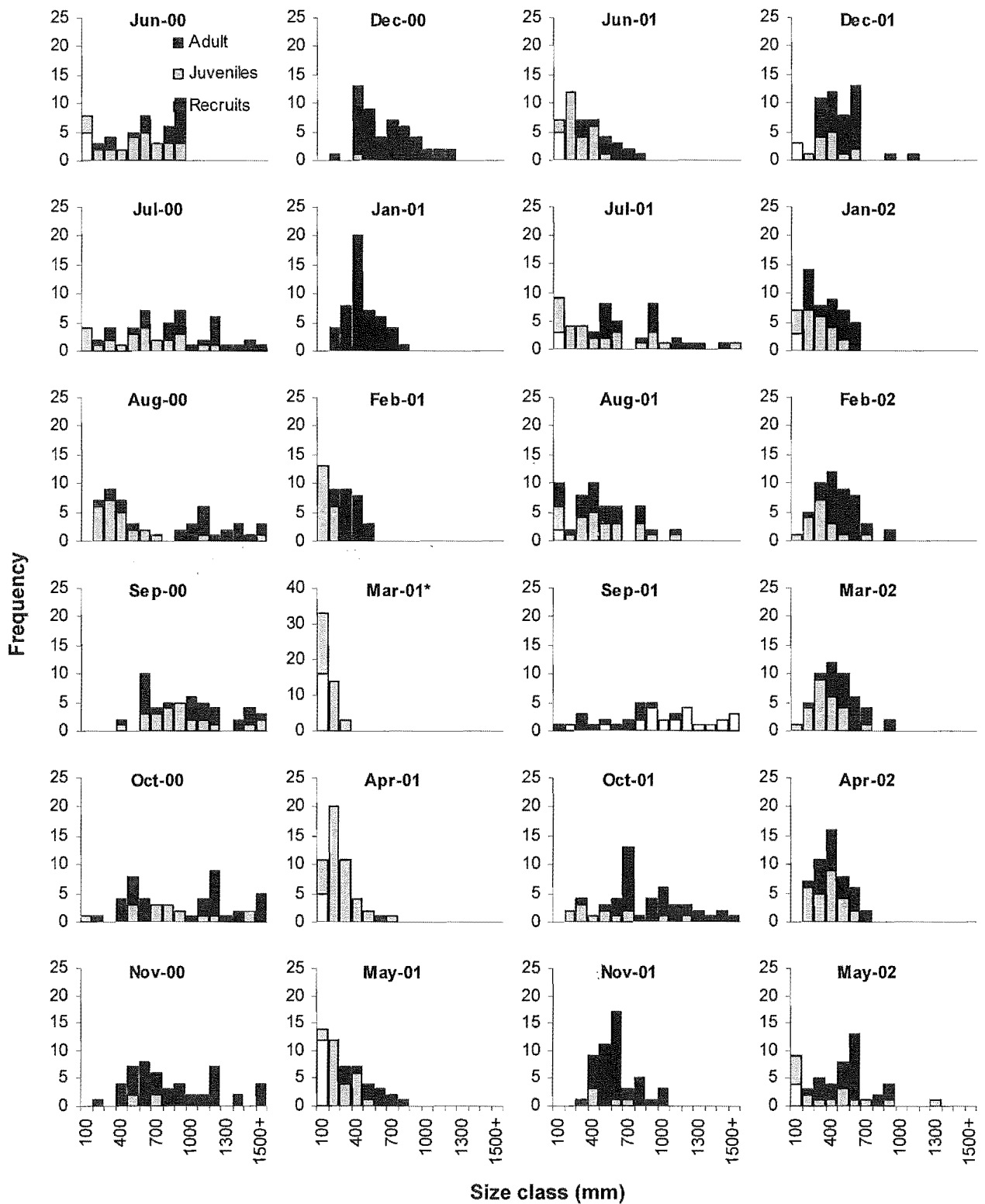


Figure A1.4: Size-frequency histograms of recruit, immature and mature *U. pinnatifida* plants from the low zone at the Moeraki Platform between February 2001 and May 2002 at quarterly intervals.  $n=50$  plants each month. Shaded bars are stacked.



**Nutrient broth**

42.5 g	NaNO <sub>3</sub>
6 g	NaH <sub>2</sub> PO <sub>4</sub>
0.26 g	FeC <sub>6</sub> H <sub>5</sub> O <sub>7</sub> ·H <sub>2</sub> O
61 g	Tris. Buffer
0.83 g	KI
31 g	H <sub>3</sub> BO <sub>3</sub>
0.25 g	Vitamin B1
0.5 mg	Vitamin B12
1 L	Distilled H <sub>2</sub> O

Culture solution diluted with seawater at a ratio of 1:1000 ml